MICROBIAL DIVERSITY THROUGH SPACE AND TIME: DISPERSAL AND DORMANCY IN MICROBIAL COMMUNITIES

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To mom, who has always believed in me and encouraged my curiosity.

Thank you for everything.

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MICROBIAL DIVERSITY THROUGH SPACE AND TIME: DISPERSAL AND DORMANCY IN MICROBIAL COMMUNITIES

Microorganisms are the most diverse organisms on the planet. Understanding the processes by which they are assembled into communities across space and time is a primary goal of microbial ecology. I employed empirical and simulation studies to investigate the effects of dispersal and dormancy on patterns of microbial biodiversity. Microorganisms are thought to have high rates of dispersal, linking communities across space to form a metacommunity. In Chapter 1, I investigated the importance of local- versus regional-scale processes for the assembly of planktonic and sediment-associated bacterial communities in a stream network. Using phylogenetic and taxonomic null models, I found habitat-specific spatial patterns of community assembly in the network, demonstrating the potentially overlooked importance of vertical habitat structure for microbial diversity in stream metacommunities. In Chapter 2, I investigated the roles of biotic interactions and dormancy for the maintenance of microbial biodiversity in University Lake, Indiana, USA. By comparing metabolically active and total diversity in a high-resolution time series, I found evidence that stabilizing biotic interactions allow taxa to persist at the local scale, aided by a dormant seed bank. In Chapter 3, I synthesized the roles of dispersal and dormancy in metacommunity ecology by analyzing empirical data and simulation models. In Chapter 4, I tested predictions about the effects of dormancy and dispersal in University Lake. Dispersal from the neighboring terrestrial ecosystem influenced diversity near the terrestrial-aquatic interface. However, most terrestrial-derived bacteria were apparently dormant, with

only a few taxa reaching high abundances in the metabolically active portion of the aquatic community. Taken together, this dissertation provides empirical demonstrations of how dispersal and dormancy affect microbial communities in nature. More broadly, it develops novel insights into the roles of dispersal and dormancy in metacommunities.

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INTRODUCTION

Earth's biodiversity is structured across scales of space, time, and biological organization. Across ecosystems and biogeographic regions, different species are favored in different environments, causing biodiversity to increase from local, to regional, to global spatial scales (MacArthur and Wilson 1967; MacArthur 1972; Rosenzweig 1995; Hubbell 2001; Worm and Tittensor 2018). Through time, diversity exhibits both short-term fluctuations in population abundances and long-term macroevolutionary dynamics due to speciation and extinction (Raup and Sepkoski 1984; Jablonski 1986; Ricklefs 2008). Importantly, these spatial and temporal patterns of diversity are not independent of one another. That is, temporal changes in diversity may depend on spatial scale or location, and spatial patterns of diversity can change through time. But these patterns of biodiversity are also influenced by the fact that species do not exist in isolation, but instead interact with one another at local scales. As such, our understanding of how biodiversity changes across space and time may be informed by the processes that regulate the structure and dynamics of ecological communities.

An ecological community consists of multiple species that are potentially interacting at a given place and time (Cody and Diamond 1975; Strong et al. 1984; Diamond and Case 1986; Morin 2011; Mittelbach 2012; Vellend 2016). Communities are structured by a suite of abiotic and biotic factors. For example, environmental conditions must good enough to allow reproduction of constituent species in a community (i.e., intrinsic growth rates must be non-negative) (Chesson 2000b; Adler et al. 2007). In addition, the net interactions with other species (e.g., via competition, consumption, or facilitation) must not negatively affect population growth rates too strongly or else populations may be driven extinct. For example, if two species exhibit poor niche differentiation, the superior competitor will displace the inferior competitor in the absence of other stabilizing forces, such as temporal fluctuations (Hutchinson 1961; Warner and Chesson 1985), trade-offs (Tilman 1982; Chase and Leibold 2003), or spatial variation (Shmida and Ellner 1984; Chesson 2000a; Ama-

rasekare 2003). Because environmental conditions and species interactions vary across space and over time, species have evolved strategies to cope with this spatial and temporal variability. Two of the most important strategies include dispersal (i.e., movement across space) and dormancy (i.e., a temporary suspension in metabolic activity) (Venable and Brown 1988; McPeek and Kalisz 1998; Buoro and Carlson 2014; Rubio de Casas et al. 2015).

Dispersal is a key process that can influence community structure and dynamics. Dispersal between spatially distinct communities links them together to form a metacommunity (Leibold et al. 2004; Holyoak et al. 2005; Logue et al. 2011; Leibold and Chase 2018). Because metacommunities contain multiple communities, they encompass multiple spatial scales and scales of biological organization. As such, metacommunity structure emerges from the cross-scale interactions that link processes operating on local scales (e.g., primarily within communities) to large scale factors (e.g., dispersal, spatial heterogeneity). The degree of spatial non-independence among local communities critically depends on the rate of dispersal in the metacommunity.

In a metacommunity, dispersal controls many aspects of community structure and dynamics. First, dispersal influences the rate at which new species arrive in a community (e.g., following a disturbance or during colonization/invasion attempts), and thus may influence temporal trajectories of local communities (Cadotte and Fukami 2005). Second, dispersal can spatially synchronize community dynamics as the effects of local biotic/abiotic interactions in one community can spill over into nearby communities, making dispersal a regional process that decouples local dynamics from local environmental constraints and biotic interactions (Mouquet and Loreau 2003; Gouhier et al. 2010). As a result, dispersal can erode spatial structure and shift control of community dynamics from local scales to the regional scale. Third, dispersal may also covary with other biologically relevant traits that have implications for community dynamics at various spatial scales. For example, trade-offs between dispersal and competitive ability can allow species that cannot coexist locally to potentially coexist at the metacommunity scale because superior colonizers and superior competitors occupy separate habitats in the face of local disturbances (Tilman 1994; Yu and Wilson 2001). Dispersal may also covary with other traits not related to competition that could have implications

for metacommunity dynamics (Rees 1993; Buoro and Carlson 2014; Wisnoski et al. 2019).

In addition to dispersal, many species can enter a reversible state of reduced metabolic activity known as dormancy. Dormancy can allow organisms to reduce the mortality associated with sub-optimal environmental conditions at the cost of delayed reproduction (Venable and Brown 1988; Bakker et al. 1996; Lennon and Jones 2011). Importantly, dormant propagules may accumulate into a "seed bank" of resting stages, each of which could potentially recolonize a community when favorable conditions return (De Stasio 1989; Pake and Venable 1996; Hairston and Kearns 2002). In this way, dormancy resembles a temporal analogue of dispersal. Consequently, dormancy can influence community structure and dynamics in a handful of ways: as a source of recolonization, as a regulator of temporal variability experienced by organisms in the community, and as a potential source of covariation with other ecologically relevant traits, such as dispersal.

I use several approaches to address questions related to the effects of dispersal and dormancy on patterns of biodiversity through space and time. I primarily rely on empirical data from bacterial communities inhabiting freshwater ecosystems. Bacteria are the most taxonomically, phylogenetically, and functionally diverse organisms on the planet, and microbial community composition differs widely across ecosystems (O'Dwyer et al. 2012; Krause et al. 2014; Martiny et al. 2015; Locey and Lennon 2016; Thompson et al. 2017; Kirchman 2018). Owing to their small size, these organisms are thought to have high rates of dispersal, but biogeographic patterns indicate dispersal may in some cases be limiting (Green and Bohannan 2006; Martiny et al. 2006; Hanson et al. 2012). In addition, many bacteria are capable of entering reversible states of dormancy, either through specialized physiological structures (e.g., endospores) or by entering phases of extreme slow growth (Lennon and Jones 2011; Lever et al. 2015; Gray et al. 2019). Due to their vast functional diversity, bacteria are responsible for key biogeochemical processes in nearly every ecosystem on Earth (Cotner and Biddanda 2002; Falkowski et al. 2008; Krause et al. 2014; Graham et al. 2016). In freshwater ecosystems, such as lakes and streams, bacteria are responsible for breaking down the complex organic matter of allochthonous inputs and consumer detritus, as well as simpler autochthonously produced compounds of aquatic phototrophs (Cotner and Biddanda 2002; Kirchman

2018). As a result, these bacteria regulate important ecosystem processes that can influence community structure by making essential nutrients (such as phosphorus, nitrogen, and silica) available to members of aquatic food webs.

In this dissertation, I investigate various roles of dispersal and dormancy in structuring ecological communities through space and time. In Chapter 1, I focus on a metacommunity with dendritic (i.e., branching, directional) network structure, which can affect dispersal rates and directionality through the metacommunity. In this chapter, I demonstrate the importance of vertical habitat structure (e.g., planktonic versus benthic habitats) for regulating the importance of local factors (e.g., species interactions and environmental filters) and dispersal for structuring bacterial communities across spatial scales in a mountain stream network. In Chapter 2, I focus more closely on the local-scale mechanisms that maintain diversity and influence community dynamics within a freshwater bacterioplankton community. In particular, I identify the joint effects of stabilizing biotic processes that generate negative frequency-dependent growth and dormancy-mediated seed bank dynamics for maintaining bacterial diversity over time. In Chapter 3, I develop a framework for integrating dispersal and dormancy into metacommunity ecology, centered around the rates of dispersal and dormancy and their degree of covariance. Using simulation models and empirical data synthesis, I evaluate the potential implications of dormancy in metacommunities. In Chapter 4, I present an empirical test of ideas developed in Chapter 3 about the ability of dormancy to buffer against suboptimal environmental conditions and affect spatial distributions in metacommunities. In particular, Chapter 5 shows how dormancy can moderate the importance of dispersal across steep environmental transitions that occur at ecosystem boundaries. In this case, I present evidence that high immigration rates of terrestrial-derived bacteria in aquatic systems may be supported by their ability to persist via dormancy, and that their implications for the metabolically active subset of the aquatic bacterial community may be minimal, particularly far from the terrestrial-aquatic interface. Overall, this dissertation uses highly diverse bacterial communities to test theoretical predictions for how ecological processes structure communities in natural systems and integrates dispersal and dormancy as drivers of biodiversity patterns from local to regional spatial scales.

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CHAPTER 1
MICROBIAL COMMUNITY ASSEMBLY IN A MULTI-LAYER DENDRITIC COMMUNITY

1.1 Abstract

A major goal of metacommunity ecology is to infer the local- and regional-scale processes that underlie community assembly. In dendritic ecological networks (e.g., stream metacommunities), branching patterns and directional flow can alter the balance between local and regional factors during assembly. Vertical habitat structure (e.g., planktonic versus benthic sediments) may further affect community assembly in dendritic metacommunities. In this study, we analyzed the bacterial metacommunity of a fifth-order mountain stream network to assess differences in community assembly (1) between planktonic and benthic habitats, (2) across spatial scales, and (3) between headwater and downstream regions of the network. Using taxonomic and phylogenetic null modeling, we found habitat-specific spatial patterns of community assembly across the dendritic network. Compositional differences between planktonic and benthic communities were maintained by divergent species sorting, but stochasticity influenced assembly at local scales. Planktonic communities showed scale-dependent assembly, transitioning from convergent sorting at local scales to divergent sorting at regional scales, while sediment community assembly was less scale dependent. While divergent sorting structured headwaters in both habitat types, sediment communities converged in structure downstream. Taken together, our results show that vertical habitat structure contributes to the scale-dependent processes of community assembly across the dendritic metacommunity.

This chapter is currently in review. A preprint has been published at bioRxiv (Wisnoski and Lennon 2020).

1.2 Introduction

Metacommunity ecology examines the assembly, structure, and diversity of communities with an emphasis on the interplay between local- and regional-scale processes (Leibold and Chase 2018). At the local scale, environmental filtering and species interactions influence assembly through species sorting (Leibold 1998; Chase et al. 2005), which leads to similar communities in similar habitats (i.e., convergent species sorting) and dissimilar communities in dissimilar habitats (i.e., divergent species sorting). The metacommunity framework also incorporates the effects of dispersal and stochastic processes on community assembly (Mouquet and Loreau 2003; Zhou and Ning 2017). For example, dispersal limitation can account for compositional dissimilarity between communities in similar habitats, while rampant dispersal can homogenize communities across dissimilar habitats due to mass effects. Therefore, species sorting should play a prevailing role in structuring communities when dispersal is low but non-limiting.

While the direction of dispersal in an idealized metacommunity is often assumed to be random, some ecosystems have physical features that impose directionality. For example, stream and river ecosystems represent dendritic networks with hierarchical, branching connectivity that constrains and directionally orients dispersal (Fig. 1.1A) (Grant et al. 2007; Brown et al. 2011; Carrara et al. 2012; Altermatt 2013). As a result, some sites in dendritic networks are more isolated and less connected than others. For example, headwater streams are separated by elongated dispersal routes along the stream network that may exceed the dispersal capabilities of some organisms. At the same time, dispersal is counteracted by prevailing downstream flows that further reduce headwater connectivity with the metacommunity (Brown et al. 2011; Altermatt 2013; Tonkin et al. 2018). Many headwater communities (e.g., benthic macroinvertebrates) are assembled by species sorting, while downstream communities show greater environmental mismatch due to high rates of dispersal from upstream (i.e., mass effects) (Brown and Swan 2010; Tornwall et al. 2017). However, different patterns have been documented for other taxonomic groups with limited upstream-dispersal vectors, such as passively dispersing microorganisms. For these communities, headwater assemblages ex-

perience high rates of immigration from surrounding terrestrial ecosystems that can disrupt species sorting (Ruiz-González, Niño-García, and del Giorgio 2015; Battin et al. 2016). Terrestrial-derived bacteria are gradually filtered out as they disperse downstream, where species sorting becomes the dominant process as stable planktonic communities establish in reaches with longer residence times (Read et al. 2015; Savio et al. 2015; Ruiz-González, Niño-García, and del Giorgio 2015; Hassell et al. 2018).

Another feature of dendritic systems that is not considered by classical metacommunity theory is that they commonly exhibit vertical habitat structure (Fig. 1.1B). In streams, planktonic organisms inhabiting the water column experience vastly different physical environments than benthic organisms living in the sediment matrix of the streambed (Hart and Finelli 1999). As a result, different sets of environmental filters may influence the composition of planktonic and benthic bacterial communities (Besemer et al. 2012; Wilhelm et al. 2013). For example, planktonic microorganisms must contend with changes in resource availability, pH, predation, and hydrology (Fierer et al. 2007; Read et al. 2015; Niño-García et al. 2016), while benthic communities experience additional constraints, such as shear stress, space limitation in biofilms, and fluctuating redox conditions resulting from surface water-groundwater mixing (Battin et al. 2016). The different flow environments of benthic and planktonic habitats could also affect bacterial dispersal rates and community assembly (Battin et al. 2016). For example, bacterioplankton presumably have high dispersal rates that increase the potential for mass effects or stochastic processes, while bacteria in sediment biofilms disperse downstream intermittently (Leff et al. 1992), increasing the potential for species sorting (Fig. 1.1C). However, the two habitats are not completely separate, as planktonic-benthic mixing introduces a vertical axis of dispersal allowing plankton to colonize sediments and sediment-associated bacteria to be suspended in the water column (Leff et al. 1992; Freimann et al. 2015), which may influence community structure at local scales. These habitat-specific differences in environmental filters and dispersal could alter the relative importance of community assembly processes underlying local and regional diversity by influencing their spatial distributions in the dendritic network.

In this study, we analyzed bacterial diversity in a dendritic metacommunity while considering not only directional flow, but also the vertical habitat structure separating stream sediments from the overlying water column in a fifth-order mountain stream network. Using taxonomic and phylogenetic approaches, we tested whether the relative importance of community assembly processes varied (1) between planktonic and benthic habitats, (2) across spatial scales, and (3) along the longitudinal (i.e., headwater versus downstream) stream dimension in the dendritic metacommunity.

1.3 Methods

1.3.1 Study site

H.J. Andrews Experimental Forest (44.2° N, 122.2° W) is a 6,400-hectare conifer forest in the Western Cascade Range, Oregon, USA. Andrews Forest is a Long-Term Ecological Research (LTER) site that contains the Lookout Creek watershed, a fifth-order, mountainous (410–1630 m elevation) catchment of high gradient streams that drains to the McKenzie River (Fig. 1.1C). The underlying geology is volcanic and dates back to the Oligocene, with Miocene-age andesite lava flows at higher elevations (Swanson and James 1975). Catchment topography is steep with confined valleys, and precipitation filters through loamy, organic soils to the stream (Harr 1977). Streams are boulder-dominated, with step–pool, riffle–pool, and cascade reaches. At lower elevations, vegetation is primarily Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Pacific silver fir (*Abies amabilis*) and noble fir (*Abies procera*) are present at higher elevations. The climate is Mediterranean, with peak precipitation between October and April. Mean annual precipitation is 230 cm at low elevations and 355 cm at high elevations (McKee and Bierlmaier 1987), and a sizeable snowpack accumulates above 900 m (Daly et al. 2010).

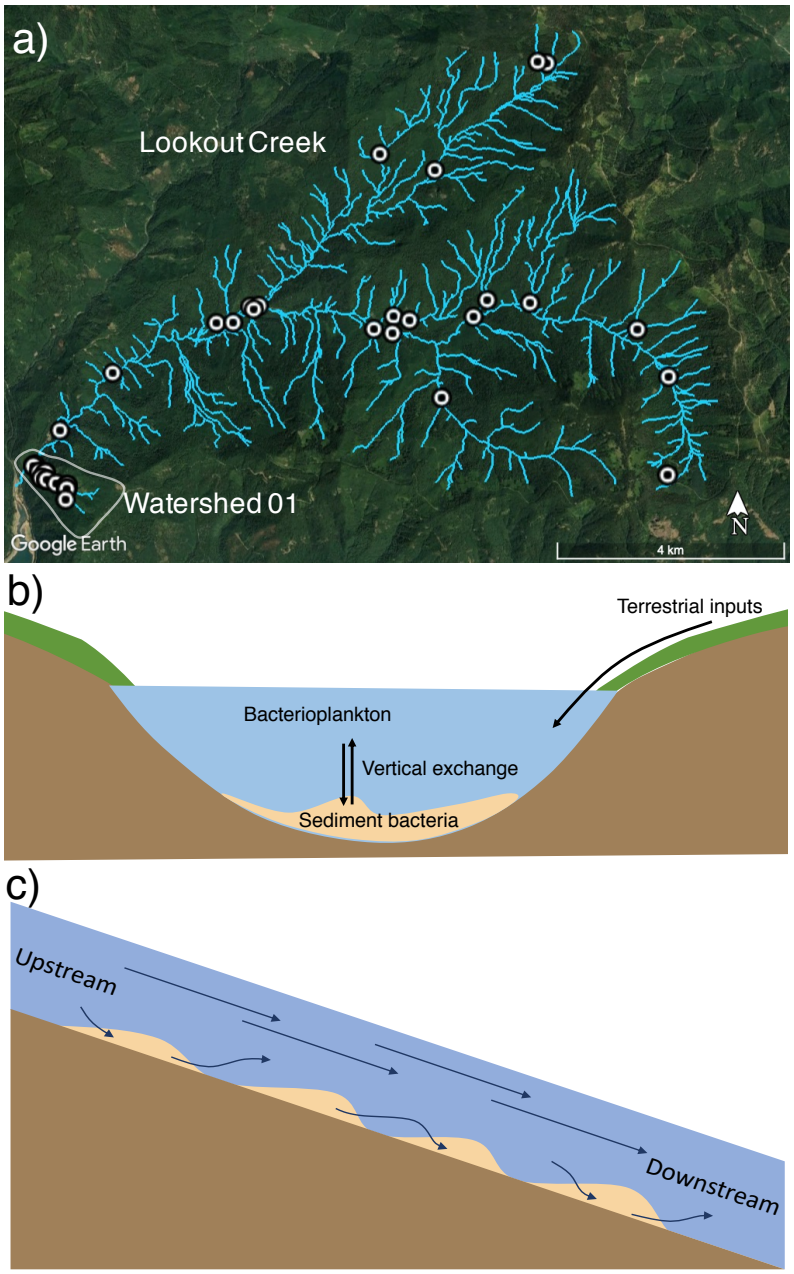

Figure 1.1: The dendritic metacommunity structure of stream ecosystems with vertical habitat structure. (a) Map of sampling locations within H. J. Andrews Experimental Forest. Sampling was conducted extensively across the broader Lookout Creek watershed, spanning stream orders 1 to 5. Sampling was also conducted intensively within small Watershed 1 (lower left). Imagery sourced from Google Earth Pro, with stream network sourced from H.J. Andrews Experimental Forest data portal. (b) A lateral cross-section through the stream channel reveals the vertical habitat structure that is present in streams. Bacterioplankton occur in the water column, while sediment-attached biofilms line the benthic habitat. (c) A longitudinal cross-section of the stream channel demonstrates the differences in spatial connectivity between planktonic and benthic habitats, where plankton are hypothesized to have higher dispersal than sediment-attached bacteria.

1.3.2 Sampling

In June 2015, we sampled streams in the Lookout Creek watershed of H.J. Andrews Experimental Forest (Fig. 1.1). Our sampling design was hierarchical, such that lower-order stream sites were nested within branches of higher-order stream sites. Our samples spanned all five stream orders of Lookout Creek, where headwaters are 1st-order streams. We sampled major confluences across the catchment. Each sampling location was geo-referenced using handheld GPS. At each site, we measured temperature, pH, and conductivity in the stream using a YSI 6920 V2-2 water quality sonde (YSI Incorporated, Yellow Springs, OH). We preserved water samples with HCl to pH 2 for chemical analyses in the laboratory. With the preserved water samples, we measured total nitrogen (TN) after persulfate digestion using the second derivative method (Bachmann and Canfield 1996) and total phosphorus (TP) using the ammonium molybdate method (Prepas and Rigler 1982). Dissolved organic carbon (DOC) was measured in 0.7-µm glass fiber filtered samples by oxidation and nondispersive infrared detection on a Shimadzu TOC-V (Kyoto, Japan). These environmental variables were used to capture longitudinal patterns in environmental conditions in the stream network.

To characterize bacterial communities, we sampled planktonic and sediment-associated microbial biomass for high-throughput community sequencing at each site. We sampled planktonic microorganisms by filtering 1 L of surface water onto 47 mm 0.2-µm Supor Filters (Pall, Port Washington, NY) in the field. We sampled sediment-associated communities (of sediment grain < 1 cm in diameter) using a sediment corer. All samples were frozen on dry ice in the field and preserved at –20 °C until processing. In the laboratory, we detached bacterial cells from sediment biofilms by gently sonicating 5 g of sediment in a 1% tetrasodium pyrophosphate solution for 10 min in pulses of 10 sec on, 5 sec off. We then used the cell suspension for downstream analysis of the sediment-associated community.

1.3.3 Sequence preparation and processing

We characterized bacterial community composition by sequencing the 16S rRNA gene (Caporaso et al. 2012). We extracted DNA from surface water samples using the PowerWater DNA isolation kit (MoBio, Carlsbad, CA) and from the sediment extractions using the PowerSoil DNA isolation kit (MoBio, Carlsbad, CA). We PCR-amplified the V4 region of the 16S rRNA gene using barcoded primers (515F and 806R) for the Illumina MiSeq platform. Per each 50 µl reaction, PCR conditions were the following: 5 µl of 10X Perfect Taq Plus PCR Buffer (5Prime), 10 µl 5P solution (5Prime), 0.25 µl Perfect Taq Plus DNA Polymerase (5Prime), 1 µl dNTP mix (10 mM each), 1 µl 515F forward primer (10 µM), 1 µl 806R reverse primer (10 µM), and 10 ng of template. Thermal cycler conditions were 3 min at 94 °C, 30 cycles of (45 sec at 94 °C, 30 sec at 50 °C, and 90 sec at 72 °C), then 10 min at 72 °C. Sequence libraries were cleaned using AMPure XP purification kit, quantified using Quant-iT PicoGreen dsDNA assay kit (Invitrogen), and pooled at equal concentrations of 10 ng per library. We sequenced the pooled libraries on the Illumina MiSeq platform at the Indiana University Center for Genomics and Bioinformatics using 300 × 300 bp paired end reads (600-cycle Reagent Kit v3). We processed the raw reads using mothur to remove non-bacterial sequences and low-quality reads (quality score < 25), and removed chimeras with VSEARCH (Schloss et al. 2009; Rognes et al. 2016). We classified OTUs with the OptiClust algorithm (Westcott and Schloss 2017) based on 97% similarity using the SILVA rRNA database version 132 (Quast et al. 2013). All further analyses were conducted in R version 3.5.3 (R Core Team 2018).

1.3.4 Diversity analysis

We analyzed taxonomic patterns of diversity within and between planktonic and benthic sediment habitats in the metacommunity. First, we rarefied each sample to a total number of 10,623 reads (the smallest sample with > 10,000 reads), and relativized reads for each OTU to the size of each sample using the R package vegan (Oksanen et al. 2019). As a measure of within-site (α) diversity, we used the exponential of Shannon's index, which corresponds to the number of equally abundant species needed to obtain the value of Shannon diversity obtained on the original data (Jost 2007).

To measure differences in community structure among sites (β-diversity), we calculated pairwise dissimilarities between communities using the Hellinger distance (Legendre and Gallagher 2001). To determine whether β-diversity was related to categorical features of the stream network, such as habitat type, stream order, and watershed, we used PERMANOVA (Anderson 2001). We used redundancy analysis (RDA) to quantify the importance of quantitative environmental variables (TP, TN, DOC, pH, elevation, conductivity) for explaining β-diversity (Legendre and Legendre 2012). We used multiple regression to quantify how community dissimilarity changed with increasing dendritic distance (i.e., along the stream network path) between sites within and between habitat types. We calculated dendritic distances in Google Earth using GIS layers of the H.J. Andrews stream network created from LIDAR imaging.

1.3.5 Community assembly processes

We used a null model approach to distinguish deterministic species sorting from stochastic assembly processes across the stream network (Chase et al. 2011; Chase and Myers 2011; Stegen et al. 2015). In this approach, we used taxonomic and phylogenetic information from the bacterial sequencing efforts (Fig. 1.2). Phylogenies organize bacterial taxa by their evolutionary history and can inform mechanisms of community assembly if broad-scale, ecologically relevant traits map onto phylogenetic relatedness (Cadotte and Davies 2016). Thus, environments may select for phylogenetically similar subsets of taxa from the metacommunity that possess traits necessary to colonize the local habitat through species sorting. Convergent species sorting (i.e., communities favoring similar taxa due to environmental similarities) was inferred when pairwise phylogenetic β-diversity was lower than expected under stochastic assembly. In contrast, divergent species sorting (i.e., dissimilar environments favoring dissimilar taxa) was inferred when phylogenetic β-diversity was greater than stochastic expectations.

To calculate phylogenetic β-diversity, we first created a phylogeny of all the OTUs in the stream network using a double-precision, approximately maximum-likelihood approach with the program FastTree v. 2.1.8 (Price et al. 2010). Using the picante R package (Kembel et al. 2010), we com-

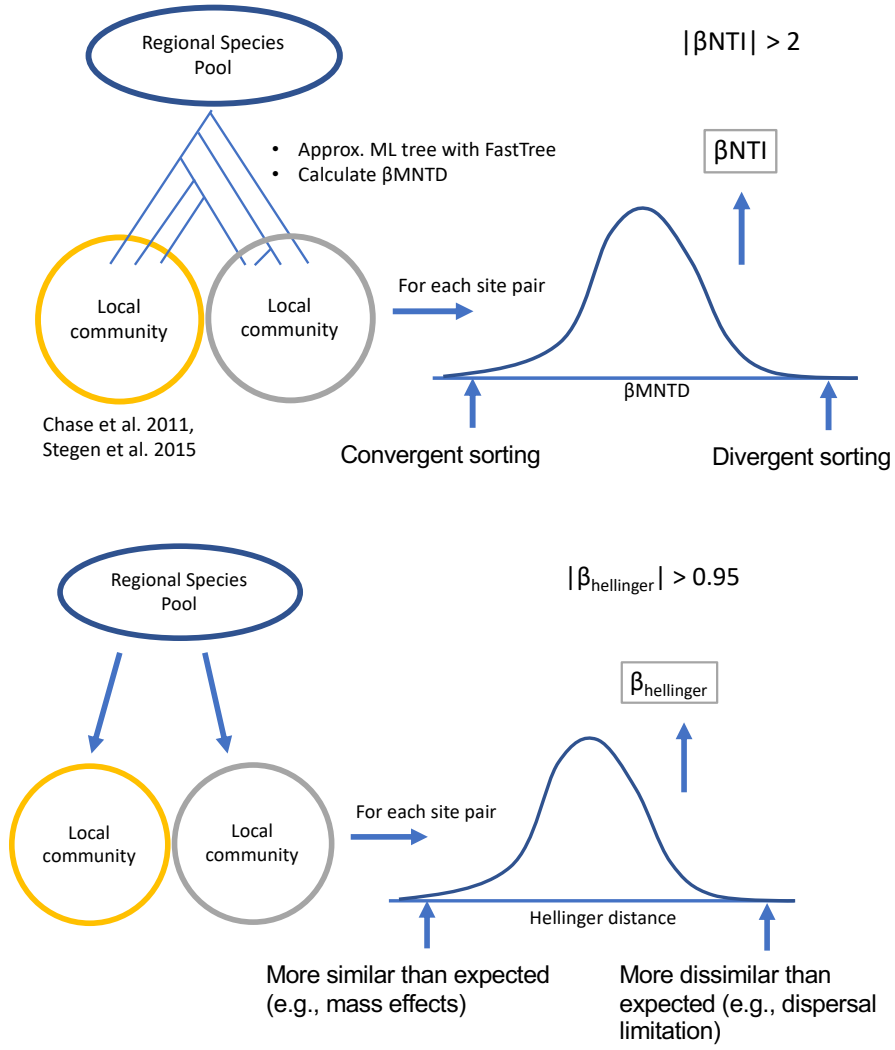

Figure 1.2: Conceptual and methodological overview of the two-step inference of community assembly in microbial communities. (A) Phylogenetic β-diversity was computed between all sites using the βNTI metric. For each site pair, observed βNTI was compared to a null distribution (n = 999) generated by shuffling tips of the phylogenetic tree. Site pairs with βNTI > 2 or < -2 were inferred to be structured by divergent or convergent species sorting. (B) In sites where species sorting was not considered a dominant process (i.e., $|\beta NTI| < 2$), inference was then made from taxonomic differences relative to a null model. The null model consisted of stochastically assembled communities from the metacommunity. Significant differences from stochasticity (calculated by comparing observed to expected Hellinger distances) were then assessed. More compositional similarity than expected was attributed to mass effects, while greater compositional dissimilarity than expected was attributed to dispersal limitation. Non-significant site pairs were assumed to have a strong influence of stochastic assembly processes.

puted the β-Mean Nearest Taxon Distance (βMNTD), an abundance-weighted community-scale measure of the mean phylogenetic relatedness of each OTU within a community compared to its most closely related OTU in a second community. We generated null distributions (n = 999) of βMNTD by randomly shuffling the tips of the phylogenetic tree. Because the contribution of rare taxa to βMNTD is small yet computationally intensive, we performed this analysis using only the OTUs detected at least 10 times in the metacommunity (n ≈ 5,700). For each pair of sites i and j, we then compared the observed βMNTD values to the null distribution for the site-pair to calculate the β-Mean Nearest Taxon Index (βNTI), which quantifies the degree of phylogenetic turnover relative to expected turnover under stochastic community assembly:

$$\beta NTI_{i,j} = \frac{\beta MNTD_{i,j} - \mu_{i,j}}{\sigma_{i,j}},$$

where $\beta NTI_{i,j}$ is the observed mean nearest taxon distance and the null distribution is described by its mean ($\mu_{i,j}$) and variance ($\sigma_{i,j}$). Thus, βNTI is a z-score, and deviations are considered significant if $|\beta NTI| > 2$, where values greater than 2 indicate divergent sorting and values less than –2 indicate convergent sorting.

To test for stochastic assembly in sites with non-significant βNTI values (i.e., weak sorting), we compared observed taxonomic β-diversity to expectations generated by a stochastically assembled null model. For a pair of sites, high dispersal should decrease β-diversity from stochastic expectations, but dispersal limitation should increase β-diversity (Chase et al. 2011; Chase and Myers 2011). To quantify the contributions of these two processes, we modified the abundance-based Raup-Crick approach of Stegen et al. (2015) to generate distributions of expected dissimilarity values for each site-pair using the Hellinger distance (n = 999 permutations). The stochastic assembly null model was performed in the following way: OTUs were randomly selected in proportion to their regional site incidence, individuals were then sequentially and randomly added to local communities in proportion to their regional relative abundances, and total abundances of assembled communities were constrained to match observed total abundances. For each pair of sites, observed Hellinger distance was compared to the site-specific null distribution to compute $\beta_{\text{RC, Hellinger}}$:

$$\beta_{\text{RC, Hellinger}} = 2\left(\frac{1 * \sum Hel_{\text{null}} > Hel_{\text{observed}} + 0.5 \times \sum Hel_{\text{null}} = Hel_{\text{observed}}}{1000} - 0.5\right),$$

where $\sum Hel_{\text{null}} > Hel_{\text{observed}}$ is the number of null Hellinger distances greater than observed values and $\sum Hel_{\text{null}} = Hel_{\text{observed}}$ is the number of ties. After this calculation, $\beta_{\text{RC, Hellinger}}$ ranges from -1 to 1. Deviations from null expectation were inferred when $|\beta_{\text{RC, Hellinger}}| > 0.95$, with $\beta_{\text{RC, Hellinger}} > 0.95$ indicating possible dispersal limitation and $\beta_{\text{RC, Hellinger}} < -0.95$ indicating potential mass effects.

1.3.6 Scale-dependent and longitudinal patterns of assembly

Finally, we investigated whether the relative importance of community assembly processes varied across spatial scales and along the longitudinal axis of the stream network. When assessing the scale-dependence of community assembly processes in the dendritic metacommunity, we only compared sites that were hydrologically connected by flow (i.e., hierarchical upstream-downstream linkages but not among hydrologically disconnected headwaters). We calculated the dendritic distance separating each pair of sites, rounding distances to the nearest log(m) to generate discrete distance classes spanning five orders of magnitude. We calculated the proportion of each assembly mechanism inferred within each distance class and quantified the frequencies of community assembly mechanisms at increasing spatial scales within and between planktonic and benthic habitats. In addition, we leveraged the nested structure of our sampling design, evaluating patterns of diversity within the overall Lookout Creek watershed and within the nested sub-watershed, Watershed 01 (Fig. 1.1A).

Because species sorting was the dominant process detected across scales in the stream network, we examined the longitudinal variation in the magnitude and direction of species sorting. Specifically, we quantified how βNTI (used to infer selection) varied with habitat type (within sediments, within planktonic samples, and between habitats) and network position (headwater streams versus

downstream) using ANOVA. The ANOVA model was constructed with βNTI values as the response variable, and with habitat type and network position as the factors. We included an interaction term to test whether the effect of network position on βNTI differs with habitat type. We then performed Tukey's HSD test to evaluate significant differences among the factors in the model.

1.4 Results

1.4.1 Patterns of α- and β-diversity

Planktonic and sediment-associated bacterial communities differed in α-diversity. On average, we observed 20% higher α-diversity in the bacterioplankton than in sediment-associated communities (species equivalents: 1789 ± 101 in sediments, 2210 ± 131 in plankton, p = 0.002, $F_{1,47}$ = 10.28). Bacterioplankton also contained > 3-fold more habitat-specific taxa (i.e., taxa never found in sediment samples) than sediment-associated communities (20.5 ± 0.9% unique in planktonic taxa vs. 6.2 ± .7% unique sediment taxa, p < 0.001, $F_{1,47}$ = 219.3).

Patterns of β-diversity suggest key differences in community structure within and between habitat types, across stream orders, and across spatial scales. Across the network, variation in bacterial community structure was explained primarily by the habitat from which the samples were taken (PERMANOVA, $R^2 = 0.12, p = 0.001$), the stream order of the sampling site ($R^2 = 0.033, p = 0.002$), and the spatial extent of the drainage basin (i.e., spanning the entire Lookout Creek watershed or the smaller, nested Watershed 01) where the samples were collected ($R^2 = 0.04, p = 0.004$). Redundancy analysis (RDA) detected a separation between bacterioplankton and sediment samples along RDA1, which explained 12% of the variation (Fig. 1.3). Along RDA2, samples separated along a gradient that captured elevation and resource availability. Specifically, we identified communities that clustered in high elevation sites with relatively high dissolved organic carbon (DOC) concentrations and communities that clustered in low elevation sites with higher total phosphorus (TP), total nitrogen (TP), conductivity, and pH. Sites in Watershed 01 also clustered together along RDA2 more tightly than sites dispersed across the broader Lookout Creek watershed.

As expected, spatially isolated sites in the dendritic network were more compositionally dis-

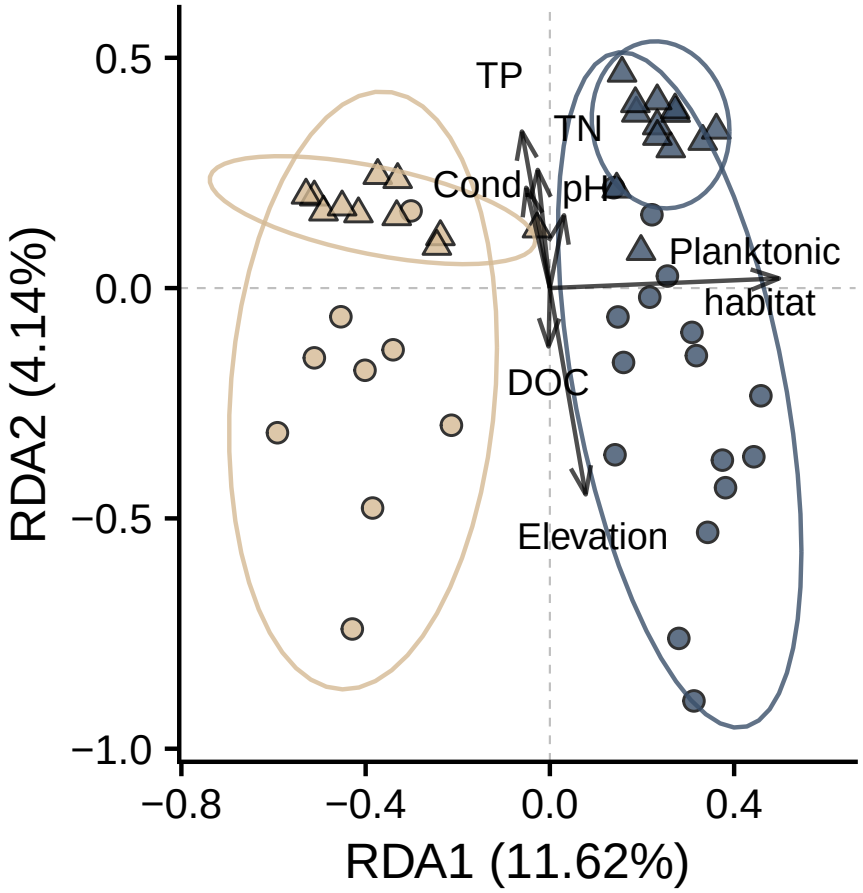

Figure 1.3: Taxonomic β-diversity revealed compositional differences among habitat types, but also within habitats. Redundancy analysis (RDA) found the primary axis of variation in community composition could be explained by habitat type (i.e., planktonic or sediment-associated). Within habitats, a secondary axis of variation explained a gradient from high elevation, low conductivity sites in the headwaters, to low elevation sites with high conductivity in the higher order streams. RDA2 also captured differences in spatial scale of sampling, with sites from Watershed 01 clustering together (triangles), nested within sites distributed across the broader Lookout Creek catchment (circles). Beige symbols indicate sediment-associated samples and blue samples indicate planktonic samples; circles indicate samples taken from the broader Lookout Creek catchment, while triangles indicate samples taken from the smaller Watershed 01 nested within Lookout Creek. Ellipses are 95% confidence intervals for the group locations in the RDA subspace.

similar than nearby sites (Fig. 1.4). However, dissimilarity increased more rapidly in planktonic than in sediment communities. The dissimilarity between communities in different habitat types was consistently higher than within-habitat differences from local (y-intercept) to regional scales ($\sim$ 10 km).

1.4.2 Scale-dependent community assembly

Bacterial community assembly in the larger Lookout Creek stream network was habitat and scale dependent. Overall, hydrologically connected communities predominantly showed evidence of convergent or divergent species sorting (620/696 = 89% of comparisons), with some evidence for stochastic assembly (54/696 = 7.8% of comparisons) or dispersal limitation (18/696 = 2.6%) (Fig. 1.5). Detection of mass effects, except at small spatial scales, was comparatively low (4/696 = 0.6% of comparisons). Within communities of the same habitat type, convergent species sorting was the dominant process (sediments: 88/134 = 66%; plankton: 142/214 = 66%). Sediment communities showed strong signatures of convergent species sorting across all spatial scales in the catchment (1 m to 10 km), with divergent species sorting playing a relatively smaller role. Within sediments, mass effects were detected at local scales (< 10 m) and stochastic effects emerged at broader (> 1 km) scales. Planktonic communities also showed evidence for convergent species sorting, but we detected divergent species sorting (32/46 = 70% of comparisons > 1 km apart) and dispersal limitation (6/46 = 13% of comparisons) at broader spatial scales. Between communities in different habitats, divergent species sorting was the dominant assembly mechanism (294/348 = 84% of comparisons), with strong stochastic effects detected at smaller spatial scales (< 100 m).

1.4.3 Longitudinal trends in community assembly

Because species sorting was the dominant process overall, we further investigated the direction (e.g., convergent or divergent) and magnitude (i.e., absolute value) of sorting inferred by βNTI along the longitudinal dimension of the stream network. We found habitat-specific trends in species sorting between headwater and downstream communities (Fig. 1.6). In the ANOVA model, net-

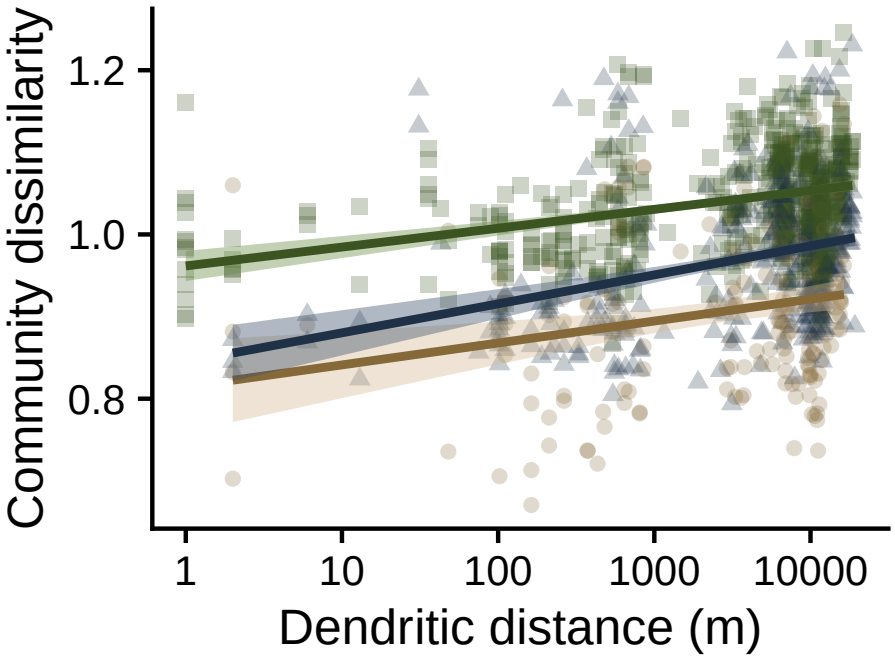

Figure 1.4: Community dissimilarity across spatial scales depended on habitat type. Community dissimilarity (using Hellinger distance) increases with dendritic distance in the network. Comparisons between sites in different habitat types (green squares, highest line) had the lowest community similarity at all spatial scales in the drainage basin. Comparisons within planktonic samples (blue triangles, middle line) were more similar at local spatial scales than between habitat comparisons ($\sim <$ 1 km), but at broader spatial scales, their dissimilarity approached that of local-scale between-habitat dissimilarity. Comparisons within benthic samples (beige circles, lowest line) were most similar across all spatial scales and their dissimilarity increased the slowest with dendritic distance.

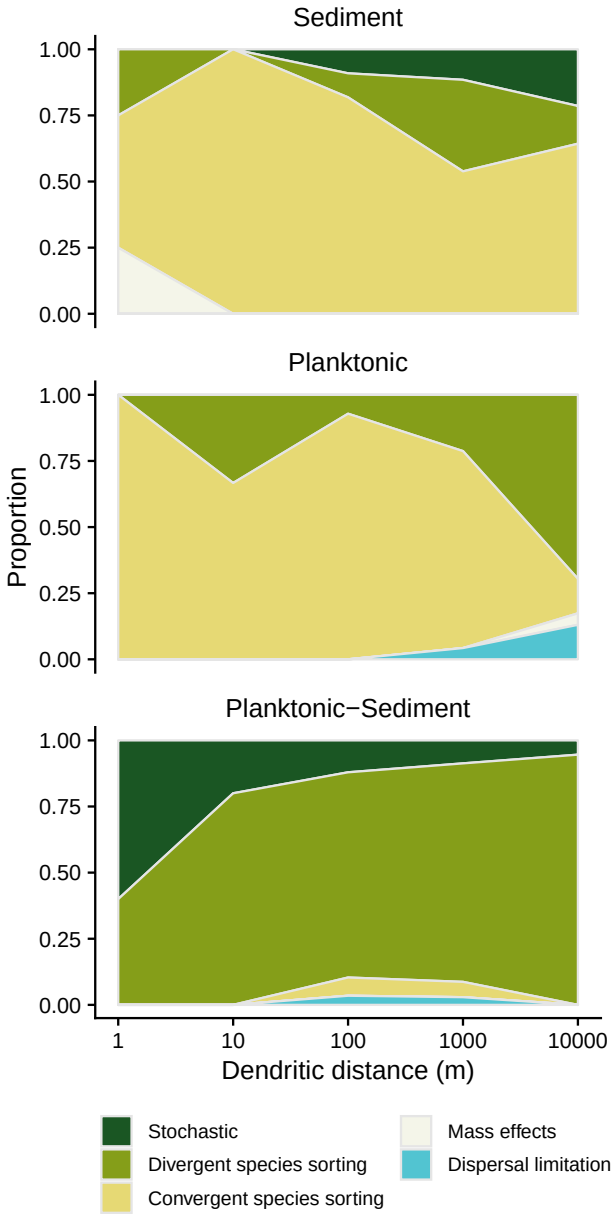

Figure 1.5: Habitat and scale dependent community assembly mechanisms in the dendritic metacommunity. In sediment habitats, convergent species sorting is the dominant assembly mechanism across all spatial scales. Divergent sorting and mass effects occur rarely at local scales, while divergent sorting and stochasticity are more common at larger scales. Within planktonic habitats, there is a transition from convergent species sorting to divergent species sorting with increasing spatial scale. Between planktonic and benthic habitats, divergent species sorting was the dominant mechanism inferred across most spatial scales, but stochasticity was common at local scales.

Table 1.1: ANOVA table for response variable βNTI with habitat and network position as predictors.

	Df	SS	MSS	F-value	p-value
Network position	1	2562	2562	36.735	2.07×10^{-9}
Habitat	2	32831	16416	235.34	$< 2 \times 10^{-16}$
Position × habitat	2	669	334	4.795	8.51×10^{-3}
Residuals	810	56499	70		

work position, habitat, and the network position × habitat interaction were all significant terms explaining βNTI in the metacommunity (Table 1.1). Using Tukey's test, we found that sorting in headwater communities was significantly divergent (i.e., |βNTI| > 2) for all comparisons within and between habitat types (mean ± SE βNTI: sediment: 8.32 ± 2.00, planktonic: 12.3 ± 1.32, planktonic-sediment: 15.2 ± 0.581). In contrast, sorting in downstream communities was significantly convergent among sediment communities (mean βNTI: -3.32 ± 0.054 SE), highly variable but stochastic on average among planktonic communities (βNTI: -1.12 ± 0.028 SE), and significantly divergent between communities in different habitats (βNTI: 11.2 ± 0.023 SE). Thus, our results suggest that the degree to which communities converge downstream depends on vertical structure.

1.5 Discussion

We have shown that bacterial community assembly in a dendritic metacommunity depends on vertical habitat structure, spatial scale, and network position. Overall, species sorting was the predominant assembly mechanism across the stream network, but the direction (e.g., convergent versus divergent) and magnitude (i.e., βNTI absolute value) of species sorting were spatially variable. Divergent species sorting maintained compositionally distinct planktonic and sediment communities (Figs. 1.3-1.6), but stochastic assembly occurred at local scales (< 1 km). Within planktonic or sediment communities, convergent species sorting was the dominant assembly process (Fig. 1.5). However, sediment-associated communities also showed evidence of local-scale (< 10 m) mass effects and broad scale (> 1 km) stochasticity, while planktonic communities transitioned from convergent to divergent species sorting with increased spatial scale (Fig. 1.5). In the longitudinal

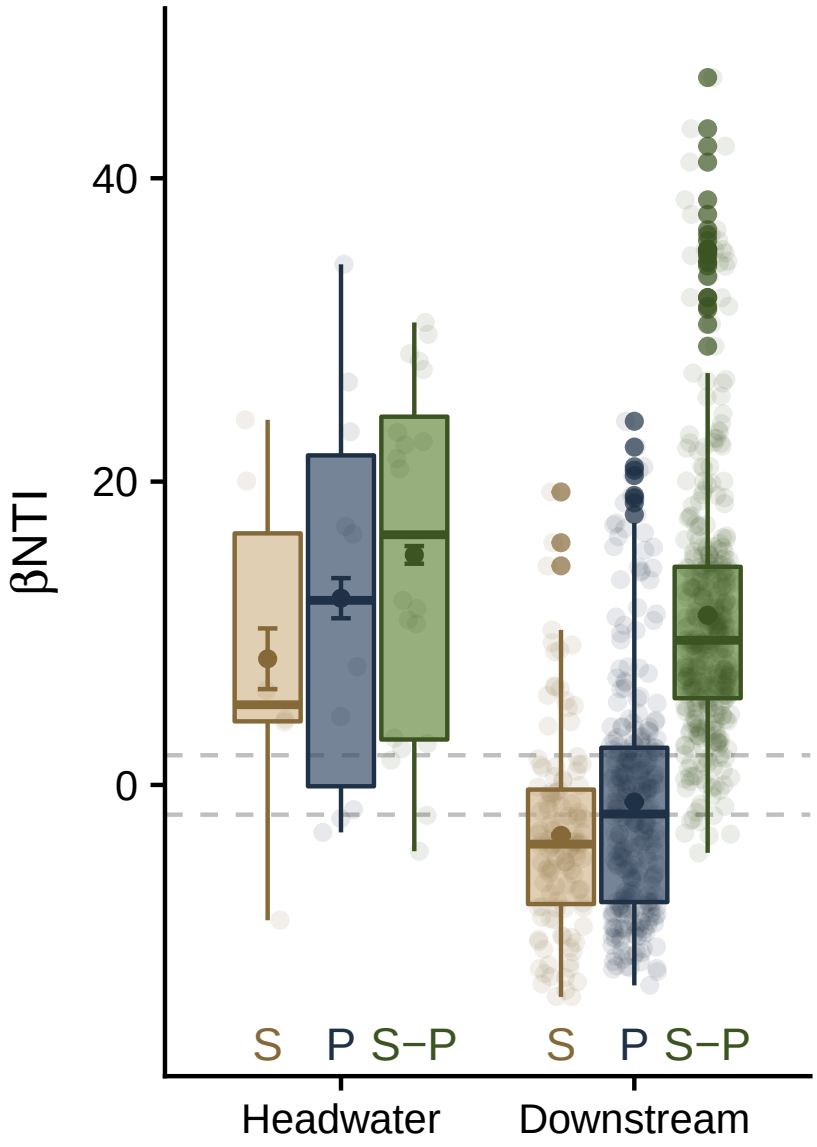

Figure 1.6: Deviations in phylogenetic β-diversity relative to null expectations (bounded by gray dashed lines) demonstrated longitudinal patterns in phylogenetic convergence or divergence between headwater and downstream sites. We compared phylogenetic β deviations within habitats (beige = sediment (S), blue = plankton (P)) and between habitats (green = sediment-plankton comparisons (S-P)). Points and error bars indicate mean ± SEM. Communities in headwaters were more phylogenetically dissimilar than expected by chance (i.e., βNTI values > 2) for all habitat comparisons, with sediment communities least divergent and between-habitat comparisons most divergent. Downstream communities showed contrasting patterns on average, with variation around the mean. On average, sediment communities were more phylogenetically convergent than expected by chance, while planktonic communities showed less deviation from stochastic expectations (mean βNTI < |2|). Downstream βNTI between habitats was lower than in headwaters, but still significantly positive on average.

dimension of the network, we detected the strongest signal of divergent sorting among headwater communities of both habitat types, while convergent sorting was most evident in downstream sediment-associated communities (Fig. 1.6). Thus, community assembly in dendritic metacommunities is strongly habitat- and scale-dependent, which may help reconcile taxonomic differences in dendritic metacommunity organization through tighter integration of spatial scale and vertical habitat structure.

1.5.1 Compositionally distinct planktonic and sediment-associated communities

Several lines of evidence support the view that deterministic processes are responsible for differences in planktonic and sediment-associated microbial communities. First, the higher α-diversity and greater proportion of habitat-specific taxa detected in the plankton suggest that many planktonic taxa do not successfully colonize the streambed. This pattern may also reflect the fact that sources other than benthic sediments (e.g., nearby soils) also contribute to planktonic diversity (Battin et al. 2016). Across the watershed, community structure was consistently distinct between planktonic and sediment habitats (Fig. 1.3), similar to what has been reported for stream bacterial communities in alpine (Besemer et al. 2012; Wilhelm et al. 2013) and arid (Kaestli et al. 2019) ecosystems. Furthermore, spatial patterns of community dissimilarity show that local-scale differences between planktonic and benthic communities can exceed within-habitat differences at larger spatial scales (Fig. 1.4). Such differences may be due to the increased stability of the sediment habitat matrix relative to the water column, as well as the physiochemical environmental differences between the two habitats (Hermans et al. 2020). In light of these results, our inferred community assembly processes (Fig. 1.5) support a prevailing role for divergent species sorting between planktonic and sediment-associated communities.

The strength of divergent species sorting between communities in different habitats was scale dependent (Fig. 1.5). At local scales, differences in community structure were partly due to stochastic processes, while divergent sorting played an increasingly large role at broader spatial scales. This scale dependence may arise from variable dispersal kernels (e.g., along preferential flow paths)

or from vertical hydrological exchange at the stream reach scale, which could generate idiosyncratic spatial variation in community structure. In our study system, it has been shown that vertical hydrological exchange plays a more important role in headwaters than in downstream reaches (Ward et al. 2019), suggesting that vertical fluxes may be responsible for disrupting the species sorting process predominantly in the headwater reaches. If so, stochastic dispersal may increase in importance downstream as channels widen and the relative importance of vertical exchange diminishes. At broader spatial scales, divergent species sorting between planktonic and benthic communities is strong enough to overcome local-scale stochasticity. Most studies have examined diversity in dendritic networks separately in either planktonic or sediment-associated communities at large scales, or through intensive sampling of both habitats at smaller spatial scales. Our combination of fine-scale sampling in the smaller Watershed 01 and broader-scale sampling in the larger Lookout Creek watershed allowed us to detect scale-dependent transitions from stochastic to deterministic assembly underlying compositional differences between habitats.

1.5.2 Longitudinal and scale-dependent transitions in planktonic community assembly

We found mixed support for the expectation that bacterioplankton community assembly is driven primarily by dispersal. The positive relationship between dendritic distance and community dissimilarity could result from dispersal, such as local-scale mass effects or regional-scale dispersal limitation, but it could also reflect species sorting along divergent environmental conditions in the watershed (Soininen et al. 2007). Divergent species sorting would be consistent with the phylogenetic patterns we observed at large spatial scales (Fig. 1.5). In our study, planktonic communities transitioned from high phylogenetic β-diversity among headwaters to lower phylogenetic β-diversity downstream, and from convergent species sorting at the reach scale (< 1 km) to divergent sorting at the watershed scale (1-10 km). Longitudinal diversity patterns reflected environmental gradients from high to low elevation sites (Fig. 1.3) that may relate to the environmental filters that influence species sorting on drifting bacterioplankton (Figs. 1.5-1.6). As previously suggested, immigration from terrestrial ecosystems can also contribute to bacterial diversity in streams, par-

ticularly in headwater reaches (Read et al. 2015; Savio et al. 2015; Ruiz-González, Niño-García, and del Giorgio 2015; Hassell et al. 2018). Mass effects of terrestrial-derived bacteria could explain phylogenetic divergence among headwaters, and why α-diversity was higher in the plankton than in sediments across the watershed. However, local-scale dispersal connectivity between terrestrial soils and bacterioplankton may be weak or transient (Hermans et al. 2020). Thus, the water column may serve as a dispersal corridor for terrestrial-derived bacteria that progressively undergo species sorting as they drift downstream.

Contrary to our expectations, we did not detect a strong signal of mass effects in the null modeling analysis of bacterioplankton communities (Fig. 1.5). We attribute this to the fact that mass effects may be difficult to distinguish from convergent species sorting without direct knowledge of dispersal rates because inferences of mass effects based on taxonomic homogenization ($\beta_{\text{RC, Hellinger}} < -0.95$) would also homogenize phylogenetic diversity (βNTI < –2). We did, however, detect dispersal limitation at the largest spatial scales (e.g., from 1-10 km), likely due to the large spatial distances between high- and low-elevation sites. For example, low-elevation headwaters of the smaller Watershed 01 were tightly clustered within the range of communities spanning the broader Lookout Creek (Fig. 1.3), which may reflect that fact that some high-elevation taxa are dispersal-limited with respect to colonizing Watershed 01 and vice versa. Thus, despite low power to detect mass effects, our results suggest that terrestrial-derived bacteria, environmental gradients, and dispersal limitation may explain changes in planktonic diversity across spatial scales and from headwaters to downstream reaches of the network.

1.5.3 Sediment community assembly shows longitudinal trends in direction despite weaker scale-dependence

In the sediment-associated communities, our results suggest species sorting may be a dominant process across a range of spatial scales (Fig. 1.5). First, sediment-associated communities were distinct from planktonic communities across the catchment (Fig. 1.3), consistent with convergent species sorting favoring the colonization of a subset of taxa from the overlying water column.

Sediment communities also showed weaker scale-dependence in community structure, as they remained more similar to each other with increasing dendritic distance than planktonic communities did (Fig. 1.4), potentially due to similar environmental filters acting across the stream network. Indeed, convergent species sorting was identified as the dominant assembly mechanism across all spatial scales of comparison (Fig. 1.4), suggesting that, in general, sediment communities consist of phylogenetically similar taxa favored by environmentally similar environments.

However, species sorting was not always convergent in sediments across the metacommunity. In particular, we observed greater phylogenetic β-diversity than expected under purely stochastic assembly among headwater sites. This signature of divergent species sorting suggests that, despite local-scale convergence within reaches (i.e., similar communities assemble within reaches, regardless of network position), different headwaters favor the assembly of phylogenetically distinct sediment communities (Fig. 1.6). This divergence among headwaters may reflect dissimilar resource inputs among headwaters draining different terrestrial areas, or spatial variation in terrestrial sources that contribute to stream sediment assembly. The transition to convergent species sorting downstream may represent longitudinal gradients in microhabitat structure (e.g., sediment size) and resource complexity (e.g., allochthonous vs. autochthonous organic matter) from lower- to higher-order streams (Vannote et al. 1980). Interestingly, we found evidence for local mass effects (e.g., 1-10 m) in the sediment communities (Fig. 1.5), which may be due to high hydrologic conductivity that mobilizes fine sediments their attached bacterial communities. The increasing frequency of stochastic assembly at the largest spatial scales (1-10 km) could reflect the idiosyncratic effects of disturbance history (e.g., large floods, debris slides, logging) that are common across the Lookout Creek watershed (Swanson and Jones 2002). Thus, while divergence is common in both sediment and planktonic communities among headwaters, sediment communities show weak scale-dependence, likely due to a more consistent set of environmental filters across spatial scales.

1.5.4 Multi-layer dendritic metacommunities

Our work provides an empirical demonstration that the community assembly processes structuring metacommunities in dendritic networks vary not only with network position, but also across spatial scales and along the vertical dimension of streams, which encompasses planktonic and benthic habitats. The joint consideration of spatial scales and vertical habitat structure may be crucial to resolving taxonomic differences in diversity patterns in dendritic metacommunities (Schmera et al. 2018). For example, aquatic taxonomic groups (e.g., riparian plants, benthic invertebrates, and microorganisms) in dendritic networks span a wide range of body sizes and generation times, disperse via different dispersal corridors throughout the stream network, and occupy benthic and planktonic habitats in vastly different ways. These key differences suggest the potential for a broader synthesis of metacommunity dynamics in stream networks built on a revised perspective embracing multi-layer dendritic networks with varying rates of dispersal and habitat use in the vertical and longitudinal dimensions.

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1.7 Publication notes

This chapter is currently in review. A preprint has been published at bioRxiv (Wisnoski and Lennon 2020). Supplemental information can be found in Appendix A.

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CHAPTER 2

STABILIZING BIOTIC INTERACTIONS AND SEED BANK DYNAMICS MAINTAIN FRESHWATER BACTERIAL DIVERSITY

2.1 Abstract

Understanding the processes that maintain biodiversity is a major aim of ecology. In general, diversity is maintained when population abundances are stabilized over time, which minimizes extinction risk by allowing populations to recover from low abundances (i.e., negative frequency-dependent growth). Stabilizing coexistence mechanisms can arise from trade-offs or from life-history strategies that capitalize on environmental fluctuations (e.g., dormancy). While demonstrated in macroorganismal communities, the importance of stabilizing mechanisms for microbial diversity in nature is less clear. In this study, we analyzed high-frequency bacterial community dynamics in a temperate lake for multiple years. Consistent with stabilization by the storage effect, we found that (1) bacterial taxa respond differently to environmental fluctuations, with maximal growth occurring at different times of the year; (2) metabolically active individuals engage in biotic interactions that generate strong negative frequency dependence among rare taxa, suggesting that stabilizing mechanisms contribute to the maintenance of diversity; and (3) population growth is buffered by seed bank dynamics, where metabolically inactive diversity accumulates during unfavorable conditions (i.e., seed bank diversity is highest in winter). Together, our results provide empirical evidence that negative frequency-dependent growth and stabilizing seed bank dynamics may be critical for maintaining microbial diversity in nature.

2.2 Introduction

An overarching goal of ecology is to understand the maintenance of biodiversity. One explanation for diversity maintenance is the high degree of specialization along various niche axes that structure

communities (May 1974; Schoener 1974). For example, this specialization may involve trade-offs in resource use (Tilman 1982; Gudelj et al. 2010; Johnson et al. 2012) or between competitive and defensive abilities (Leibold 1996; Thingstad et al. 2014; Cadier et al. 2019). These stabilizing niche differences can prevent competitive exclusion, allow populations to recover from low abundances, and maintain diversity (Chesson 2000b; Adler et al. 2007). Stabilization can also emerge at larger spatial or temporal scales. For instance, spatial heterogeneity favors different species in different locations, which can maintain diversity at regional and landscape scales (Amarasekare 2003; Martiny et al. 2006; Hanson et al. 2012; Hart et al. 2017). Likewise, temporal fluctuations can maintain diversity via oscillating, seasonal community dynamics, such that species are favored at different times (Pake and Venable 1996; Kent et al. 2007; Gilbert et al. 2012; Fuhrman et al. 2015). Although stabilizing coexistence has been demonstrated in plant and animal communities (Cáceres 1997; Angert et al. 2009; Adler et al. 2013), few studies have documented stabilizing coexistence mechanisms for microorganisms (Jiang and Morin 2007; Zhang et al. 2010), especially in nature.

Diversity is maintained when population abundances are stabilized over time, thereby decreasing the risk of extinction. This arises when there is stronger intraspecific than interspecific competition, which generates negative frequency-dependence (NFD) in population growth. The result of NFD is that that populations grow faster when rare than when common (Chesson 2000b; Adler et al. 2007). Without stabilization, populations lack a refuge in rarity and decline to extinction via positive feedbacks. Given that microbial communities contain a disproportionately large number of rare taxa (Sogin et al. 2006; Lynch and Neufeld 2015; Shade et al. 2018), NFD may be an important but overlooked process for maintaining the exceptional diversity discovered across the microbial domains of life. While some of these rare taxa exhibit conditional rarity (e.g., some copiotrophs) (Shade et al. 2014), others appear to persist at low abundances across longer timescales (e.g., some oligotrophs) (Alonso-Sáez et al. 2015; Lynch and Neufeld 2015; Newton and Shade 2016). These persistently rare taxa may be important contributors to microbial diversity, but it is unclear how they stably coexist in the community. One hypothesis is that strong NFD prevents persistently rare taxa from reaching high relative abundances, while also providing them with a greater refuge when

rare (Fig. B.4), thereby promoting stable coexistence (Yenni et al. 2012, 2017; Rovere and Fox 2019).

Stabilization can arise from life-history strategies that facilitate recovery from rarity and help maintain diversity. In fluctuating environments, diversity can be maintained by the storage effect (Warner and Chesson 1985; Chesson 2000b), which occurs when taxa differ in their responses to environmental conditions, when competition peaks during favorable conditions, and when population growth is buffered during suboptimal conditions (Pake and Venable 1996; Cáceres 1997; Angert et al. 2009). Conditions for the storage effect may be satisfied when taxa experience extremely slow growth (Gray et al. 2019) or engage in various forms of dormancy, which are common among microorganisms (Lennon and Jones 2011). The accumulation of dormant individuals in a "seed bank" can not only reduce extinction when rare, it can also facilitate the resuscitation and subsequent growth of populations when favorable conditions return. Seed bank dynamics also contribute to NFD because emergence from the seed bank generates disproportionately large increases in the active population sizes of rare versus common taxa. Therefore, distinguishing NFD among taxa with different metabolic states should provide insight into the mechanisms that maintain microbial diversity.

In this study, we analyzed bacterioplankton dynamics in a temperate lake at high temporal resolution to infer the ecological processes that maintain diversity. We determined whether persistent (and potentially coexisting) taxa differentially respond to environmental fluctuations, suggestive of temporal niche partitioning. We then used null models to assess whether stabilizing biotic mechanisms (e.g., stronger intraspecific than interspecific competition, as evidenced by strong NFD) help maintain rare taxa in the community (Yenni et al. 2017; Rovere and Fox 2019). We compared patterns of NFD and population dynamics in the active and total portions of the community (inferred by 16S rRNA transcripts and genes, respectively) to understand the importance of buffered population growth strategies, such as slow growth or dormancy, for the maintenance of diversity. Consistent with predictions from the storage effect, our results provide empirical evidence that stabilizing biotic interactions and buffered population growth may fuel seasonal community dynamics

and play key roles in maintaining bacterial diversity in natural ecosystems.

2.3 Methods

2.3.1 Study site and sampling

University Lake is a 3.2 ha meso-eutrophic reservoir located in the Indiana University Research and Teaching Preserve, Bloomington, Indiana, USA (39°11' N, 86°30' W). The surrounding forest is dominated by oak, beech, and maple. Three streams drain into University Lake, which has an estimated volume of 150,000 m^3 and a maximum depth of 10 m. From April 2013 to September 2015, we took weekly water samples from the surface (0-0.5 m) of the epilimnion of University Lake for microbial biomass, total phosphorus (TP), total nitrogen (TN), and dissolved organic carbon (DOC). Microbial biomass was filtered on 0.2 μm Supor filters (Pall, Port Washington, NY, USA) and frozen at -80 °C. We quantified TP using the ammonium molybdate method (Wetzel and Likens 2000) and TN with the second derivative method after persulfate digestion (Crumpton et al. 1992). DOC was quantified following 0.7 μm filtration using nondispersive infrared (NDIR) detection on a Shimadzu TOC-V (Kyoto, Japan). We quantified water transparency with a Secchi disk and used a Quanta Hydrolab (OTT, Kempton, Germany) water sonde to measure temperature, conductivity, dissolved oxygen, salinity, and pH in the lake.

2.3.2 Bacterial community structure

We characterized total and active bacterial community structure by sequencing 16S rRNA genes (DNA) and transcripts (RNA), respectively. We extracted total nucleic acids from 0.2 μm filters using the MoBio PowerWater RNA extraction kit and the DNA elution accessory kit. We prepared DNA libraries to identify taxa that were present in each bacterioplankton community sample. Because sequences obtained via DNA can come from metabolically active or inactive (e.g., slow growing or dormant) individuals, this sample represents the "total" community. In contrast, rRNA is a more ephemeral molecule produced by growing cells; therefore, it is often used to characterize

the metabolically "active" subset of the community (Molin and Givskov 1999; Steiner et al. 2019; Locey et al. 2020). We used DNase (Invitrogen) to remove DNA from the RNA extractions and then synthesized cDNA with SuperScript III First Strand Synthesis kit and random hexamer primers (Invitrogen). To amplify the 16S rRNA gene (DNA) and transcript (cDNA), we used barcoded V4 primers (515F and 806R) designed for the Illumina MiSeq platform (Caporaso et al. 2012). We then purified the PCR products with AMPure XP, quantified DNA concentrations using PicoGreen, and pooled samples at 10 ng per sample. The resulting libraries were sequenced on an Illumina MiSeq at the Indiana University Center for Genomic and Bioinformatics Sequencing Facility using 250 × 250 bp paired end reads (Reagent Kit v2). Paired-end sequences were subsequently processed in the software package mothur (version 1.41.1, Schloss et al. 2009). We assembled contigs, removed low quality sequences (minimum score of 35), aligned sequences to the Silva Database (Version 132) (Quast et al. 2013), removed chimeras using the VSEARCH algorithm (Rognes et al. 2016), and created 97% similar operational taxonomic units (OTUs) using the OptiClust algorithm (Westcott and Schloss 2017), assigning taxonomy with the RDP (Cole et al. 2009). To account for variation in sequencing depth, subsequent analyses were performed on rarefied abundance data subsampled to the fewest number of reads in the time series (N = 5979 per sample) using R v. 3.6.0 (R Core Team 2018).

2.3.3 Differential responses to environment

We inferred the role of environmental fluctuations for maintaining diversity by characterizing whether taxa respond differently to the environment, the first criterion of the storage effect. We performed a principal component analysis (PCA) on Hellinger-transformed abundances to visualize seasonal patterns of compositional trajectories. We identified environmental drivers of community dynamics using redundancy analysis (RDA). We computed the correlation between environmental vectors and species scores along RDA axes to identify the environmental drivers of specific OTU relative abundances. To determine whether environmental fluctuations facilitate temporal niche partitioning, we identified the week of the year when each persistent OTU experienced its

maximum average growth rate (using calculations defined in the following subsection).

2.3.4 Stabilizing biotic interactions

We tested whether stabilizing mechanisms contribute to the maintenance of diversity by calculating whether rare taxa experienced stronger negative frequency dependence than common taxa (Yenni et al. 2017). This condition relates to the second criterion of the storage effect by determining whether rare taxa may experience the strongest intraspecific competition during the period of the year when they are environmentally favored, which would generate NFD. First, we focused only on the taxa that persisted across the time series by selecting the OTUs present in 80% of the total community (DNA-based) samples. Transient species were, by definition, not persistent and may not meaningfully engage in long-term species interactions, so we excluded them from the analysis (Yenni et al. 2017). We retained 82 persistent OTUs (Table B.1). We then focused on the subset of the active community (RNA-based) that contained these same OTUs. We inferred the strength of negative frequency dependence of an OTU as the magnitude of the negative slope of the relationship between an OTU's relative abundance and its per capita growth rate at each time step (t) across the time series. We calculated the relative abundance ($x_{t,s}$), of each OTU (s) as its abundance ($N_{t,s}$) in the community of s OTUs relative to the total abundance of all s OTUs ($\sum_s N_{t,s}$) at a given time step (t), such that $x_{t,s} = \frac{N_{t,s}}{\sum_s N_{t,s}}$. We calculated the natural log of the per capita growth rate of each OTU as $y_{t,s} = \log_e \left(\frac{N_{t+1,s}}{N_{t,s}}\right)$. To estimate the strength of negative frequency dependence for each OTU, we fit simple linear regressions ($y_s = \beta_{0,s} + \beta_{1,s}x_s + \epsilon_s$), where the equilibrium frequency of an OTU (f) is the x-intercept, $f = -\frac{\beta_{0,s}}{\beta_{1,s}}$, and the degree of frequency dependence (NFD) is the slope $NFD = \beta_{1,s}$. In the end, f describes whether an OTU is common or rare, and negative slopes with greater magnitudes indicate stronger negative frequency dependence.

Stabilization of rare taxa by NFD would be supported if OTUs with greater equilibrium frequencies (larger values of f) had less negative slopes (smaller $|\beta_{1,s}|$), which we inferred from the magnitude of negative covariance between the $\log(NFD)$ and $\log(f)$. To account for the fact that the expectation of this covariance is already negative and to control for spurious statistical correla-

tions in the temporal data due to other factors, we implemented a null model approach (Yenni et al. 2017). We shuffled the abundances of each OTU independently, recalculated relative abundances and per capita growth rates, estimated equilibrium frequencies (fs) and negative frequency dependences (NFDs), and calculated the covariance, repeating this procedure 5000 times to generate a null distribution of covariance values ($COV[\log\ (f), \log\ (NFD)]$) (Yenni et al. 2017). We then compared our observed covariance with the null distribution to infer the strength of asymmetrical negative frequency dependence (i.e., the degree to which rare OTUs experience disproportionately stronger self-limitation than common OTUs). We calculated standardized effect sizes (SES = mean observed covariance / standard deviation of covariances in the null distribution) as well as the ratio of observed covariance to the average covariance of the null distribution (Yenni et al. 2017), where more negative SES and larger ratios indicate greater deviations from the null expectation of equal NFD across taxa. We inferred the degree of statistical significance by calculating a p-value as the proportion of null covariance values less than or equal to our observed covariance.

2.3.5 Seed bank dynamics

Next, we analyzed the importance of the seed bank for maintaining diversity via buffered population growth, the third criterion of the storage effect. First, we examined whether the seed bank was a reservoir of taxonomic diversity by comparing the ratio of total richness to active richness at each time point in the time series, where larger ratios indicate that the total community has higher α-diversity than the active subset of the community. We then sought to classify the 82 persistent OTUs by their reliance on the seed bank. We developed a reactivation metric to quantify each OTU's frequency of reactivation from the seed bank. For each OTU, its reactivation score is the number of times where an OTU is present (i.e., detected in the DNA pool) but inactive (i.e., absent from the RNA pool) at time point *t*, yet active (in the RNA pool) at time point *t+1*. This represents a transition from the inactive to active state mediated through slow growth or dormancy. Thus, OTUs with higher reactivation scores may be more reliant on the seed bank for long-term persistence in the community. We then analyzed the relationship between the average relative abundance of OTUs

and their reactivation score to determine whether seed banking was more important for maintaining rare taxa than common taxa in the bacterioplankton community.

2.4 Results

2.4.1 Differential responses to environment

Bacterial community dynamics were related to environmental variability, such that different taxa were favored at different times of the year. During the summer months, the community followed a recurrent successional trajectory (Fig. 2.1A). This trajectory aligned with seasonal trends in temperature (Fig. 2.1B; a summary of environmental variation is provided in Fig. B.1). Across longer time scales, inter-annual variation in pH was associated with compositional differences in the active bacterial community during winter months. Within an annual cycle, the persistent OTUs (n = 82) demonstrated temporal partitioning in their maximal growth rates in the active portion of the community (Fig. 2.2, Table B.2), corresponding to different environmental conditions (Fig. B.2).

2.4.2 Stabilizing biotic interactions

Persistent taxa exhibited stabilizing NFD (Fig. B.5), which varied in strength depending on each taxon's mean relative abundance in the community (Fig. 2.3). In particular, NFD was significantly stronger for rare taxa than common taxa, but only in the active portion of the community ($p = 0.0002$; $SES = -4.03$, covariance ratio $= 1.08$), not in the total community ($p = 0.221$; $SES = -0.777$, covariance ratio $= 1.01$). The p-values reflect the rank of observed NFD compared with null simulations, while SES values take into account the variance in the null distribution. In other words, the total community showed nearly the same degree of stabilization (|SES| < 2, covariance ratio ~ 1) as the null communities. The degree to which rare taxa were more strongly stabilized by NFD was qualitatively robust to the number of taxa included in the analysis (Fig. B.9).

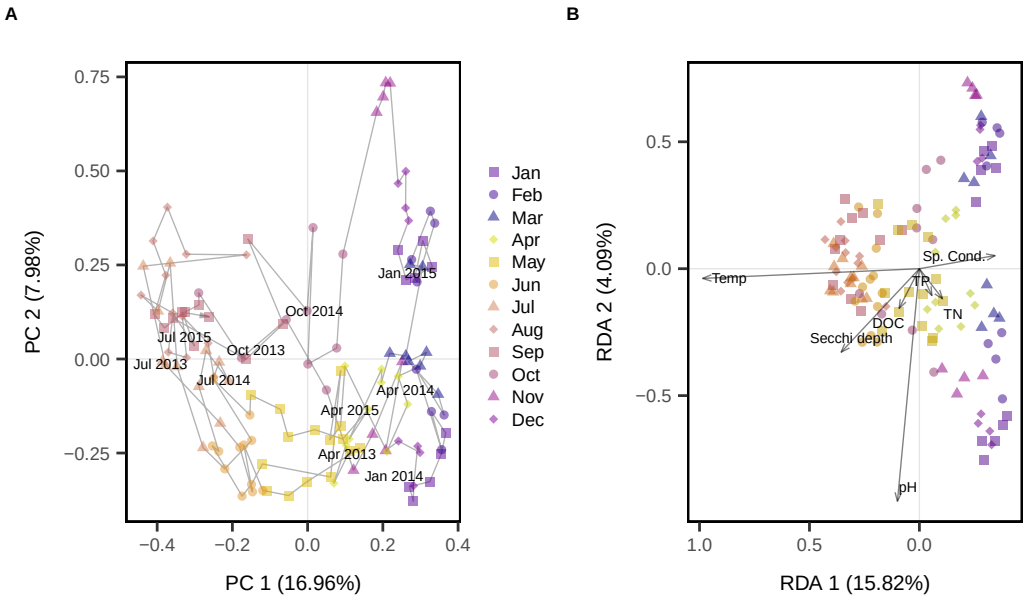

Figure 2.1: Seasonality of active community dynamics. (A) The compositional trajectory of the active community shows strong seasonality, but the community remains relatively static over winter. The first two axes of the principal component analysis (PCA) depict summer/winter differences (PC1) along the major axis, and slight inter-annual differences in winter composition (cool colors) along the minor axis (PC2). The summer successional trajectory (warmer colors) is highly repeatable and months have similar community structure among years. (B) Constrained ordination using redundancy analysis (RDA) shows the environmental drivers of community structure, along with strong correlates of individual taxa in the community. This analysis reveals that differences in pH may explain variation in winter composition among years.

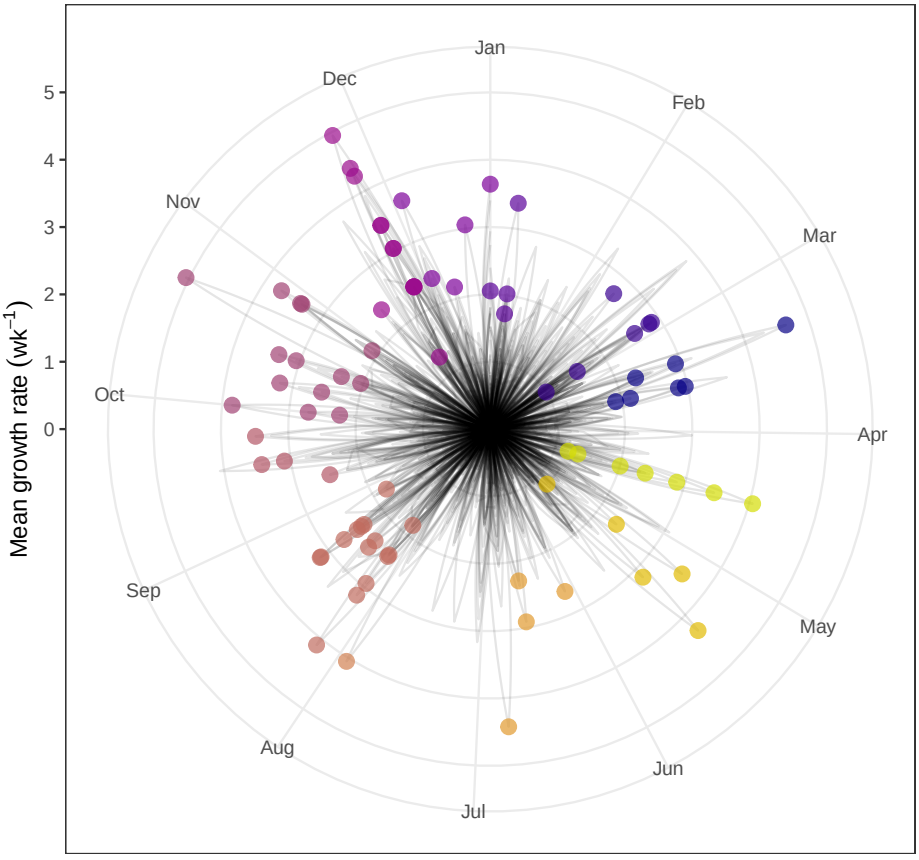

Figure 2.2: Temporal partitioning of maximum growth rate among persistent taxa. Lines represent the mean weekly growth rate for each taxon over the time series. Points indicate the maximum growth observed for each OTU. Overall, the 82 persistent OTUs have maximum growth rates at different portions of the year (see Table B.2). The color scheme is the same as in Figure 1, where yellow represents the month of April, warmer colors represent summer months, and cooler colors represent winter months.

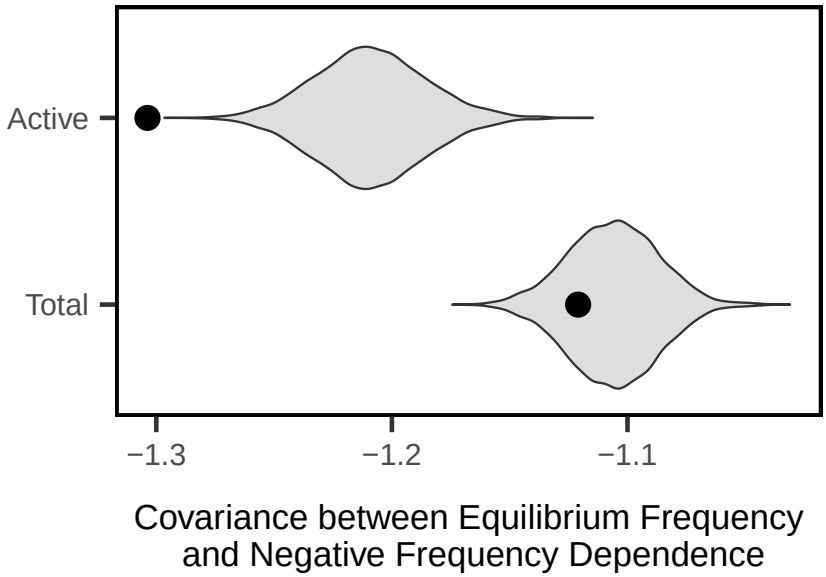

Figure 2.3: Negative frequency dependence for 82 persistent bacterial taxa is stronger in rare than common taxa, but only in the active portion of the community. The standardized effect size (SES) of the covariance in the active portion of the community was -4.03, while the total community SES was -0.77. The overall strength of NFD (observed NFD / mean NFD) was 1.08 in the active portion and 1.01 in the total community.

2.4.3 Seed bank dynamics

Our data suggest seed banks of dormant or slow growing individuals contribute to the maintenance of diversity. Over the course of our study, total richness ranged from $\sim$1.2–2 times higher than the richness of the active portion of the community (Fig. 2.4). Furthermore, this discrepancy between total and active richness exhibited seasonality, demonstrating a time-varying role for the bacterial seed bank. In particular, the seed bank played a weaker role (i.e., active and total richness were more similar in magnitude) during the summer, while proportionally higher diversity was found in the seed bank over winter, when growing conditions may be less optimal (Fig. 2.4).

Generally, the taxa that exhibited more reactivations from the seed bank were also the taxa that were, on average, consistently rare in the active portion of the community (Fig. 2.5). In contrast, common taxa exhibited fewer transitions between active and inactive states in the community. Thus, in addition to experiencing strong NFD when metabolically active, persistently rare taxa in

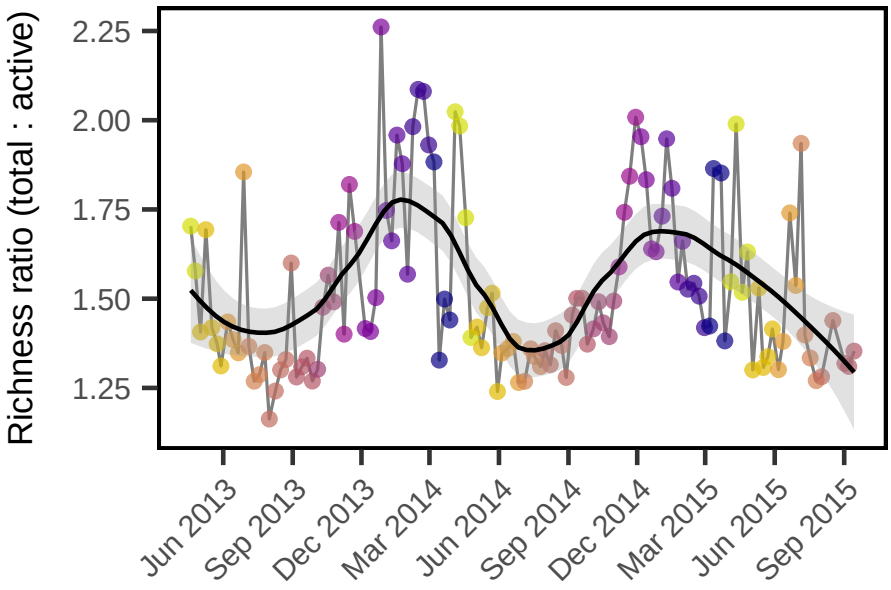

Figure 2.4: Seasonal importance of the seed bank. Diversity is much higher in the total community, relative to the active community, during the fall and winter months. The active and total communities converge over the summer, indicated by values on the y-axis closer to 1. The color scheme is the same as in Figure 1, where yellow represents the month of April, warmer colors represent summer months, and cooler colors represent winter months.

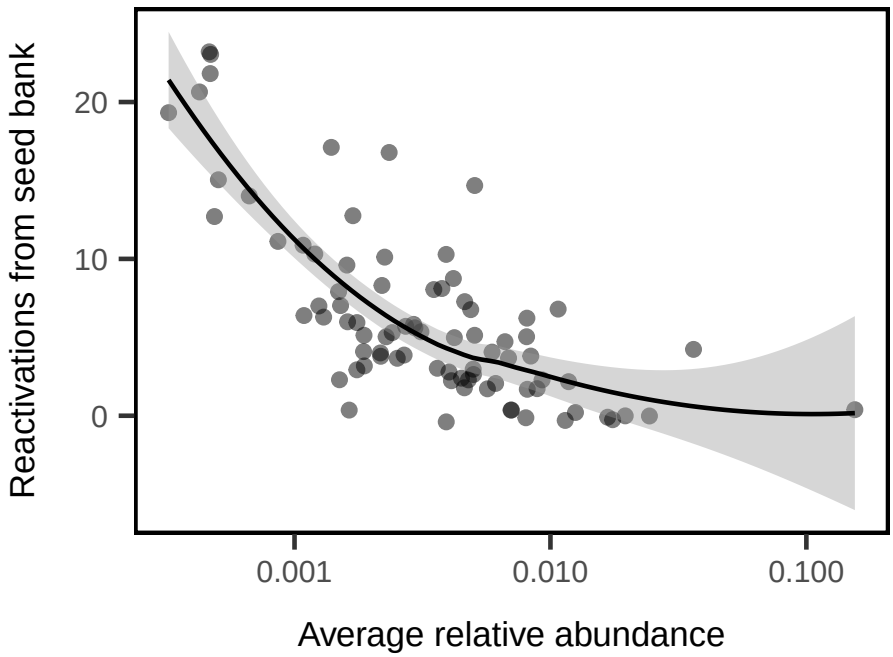

Figure 2.5: Rare taxa showed more seed bank transitions. For the 82 persistent taxa identified over the time series, OTUs that were (on average) rare in the active portion of the community had a higher number of reactivations from the seed bank, while more common taxa had fewer reactivations. The fit was performed via locally estimated scatterplot smoothing (LOESS).

the community also appear to rely on life history strategies, such as slow growth or dormancy, to avoid extinction in the community.

2.5 Discussion

Biodiversity in a freshwater bacterioplankton community was maintained by stabilizing ecological processes that generate negative frequency dependence (NFD). High resolution sampling revealed recurrent seasonality in community dynamics that tracked environmental conditions (Fig. 2.1). These temporal dynamics may be driven by differential responses to the environment, as different taxa exhibited maximum growth rates at different times of the year (Fig. 2.2, Fig. B.2). Differential responses to environmental conditions also contributed to biotic interactions (e.g., stronger intra- than interspecific competition) that stabilized population dynamics in the community (Fig. B.5), such that NFD was stronger in rare than common taxa (Fig. 2.3). Importantly, this strong NFD was

not detected in the total community that included inactive bacteria, suggesting biotic interactions by rare, but metabolically active, individuals may be crucial for maintaining diversity. Furthermore, the maintenance of diversity may be enhanced by life-history strategies, such as dormancy, that buffer rare taxa from extinction during environmentally unfavorable periods (e.g., winter) (Fig. 2.4-2.5). Consistent with predictions from the storage effect, these findings reveal a combination of stabilizing mechanisms that contribute to the maintenance of bacterial biodiversity in nature.

2.5.1 Negative frequency dependence in microbial communities

We found evidence for stabilization through negative frequency dependence (NFD). In particular, disproportionately strong NFD was detected for rare taxa, offering a potential explanation for why some taxa appear to stably persist at low relative abundances in nature (Alonso-Sáez et al. 2015; Lindh et al. 2015), potentially as members of the "rare biosphere" (Sogin et al. 2006; Lynch and Neufeld 2015; Shade et al. 2018). Asymmetric NFD is also important for the coexistence of rare plant and animal species, but the magnitude of this effect varies across taxonomic groups (Yenni et al. 2017; Rovere and Fox 2019). For example, NFD is less asymmetric for herpetofauna than plant or mammal communities (Yenni et al. 2017), possibly due to higher evenness in herpetological communities (Rovere and Fox 2019). Compared to macro-organismal systems, the degree of NFD asymmetry in our highly uneven bacterial community was moderate, suggesting additional factors (e.g., seed banks) may be important in this system. However, our comparison between the metabolically active and total portions of the bacterioplankton community provides critical evidence that active organisms mediate the biotic interactions that generate asymmetry in NFD and maintain diversity. Consistent with prior work showing that rare taxa may be disproportionately active (Jones and Lennon 2010), our study demonstrates that rare, but active, bacteria engage in biotic interactions that could allow them to stably persist in the community.

2.5.2 Storage effects in microbial communities

Temporal niche partitioning mediated by seed bank dynamics may explain the maintenance of diversity in fluctuating environments. In the temperate climate of our study lake, different bacterial taxa in the lake exhibit maximum growth rates at different times of the year (Fig. 2.2), which coincide with different environmental conditions (Fig. B.2). As a result, different taxa are favored under different environmental conditions, which may explain the recurrent summer dynamics of the active community (Fig. 2.1). Recurrent community dynamics could be facilitated by dormant seed banks, which may be critical for coping with seasonal environmental fluctuations (Pake and Venable 1996; Hellweger et al. 2008). Evidence for the role of seed banks in this system comes from (1) the lack of asymmetric NFD in the total community (Fig. 2.3), suggesting inactive bacteria weaken the relationship between growth and biotic interactions; and (2) the seasonality of the seed bank (Fig. 2.4), where storage in the seed bank is maximized when environmental conditions (e.g., water temperature, resource/consumer densities) are least favorable for bacterial growth (Neuenschwander et al. 2015). Overall, these patterns suggest that recurrent environmental cues regulate active community dynamics by favoring different taxa at different times, and that seed banks are potentially important for maintaining these seasonal community trajectories.

While difficult to demonstrate definitively, the storage effect is often invoked as a potential explanation for species coexistence in fluctuating environments when the species involved have the potential to enter dormancy. The fundamental requirements for the storage effect are that species (1) show differential responses to environmental conditions, (2) experience increased intraspecific competition during the most favorable periods for growth, and (3) exhibit buffered population growth that leads to overlapping generations (Chesson 2000b). In our study, different bacterial taxa showed maximum population growth under different environmental conditions (Fig. 2.2), species showed negative frequency dependence in their growth such that they experienced greater self-limitation (consistent with stronger intraspecific than interspecific competition) when they had greater relative abundances (Fig. 2.3), and the contrasting dynamics between active and total communities suggested the presence of buffered population dynamics via the maintenance of dormant

propagules (Fig. 2.4). While these conditions are not definitive proof of a storage effect acting in our study system, they are consistent with the criteria needed for storage effects to contribute to the long-term maintenance of diversity.

2.5.3 Future directions and conclusions

Our study provides empirical evidence that biotic mechanisms stabilize bacterial communities and maintain diversity. While our results indicate differences in the diversity, dynamics, and stabilization between active and total subsets of the community, an ultimate goal is to tighten the mechanistic links between rates of ribosomal RNA transcription and *in situ* growth rates for individual taxa (Newton and Shade 2016; Papp et al. 2018). While it also may be important to consider the effects of dispersal in some systems (Crump et al. 2012), previous work in our study system found that most immigrating taxa are metabolically inactive (Wisnoski et al. 2020). Thus, one explanation for the lack of asymmetric NFD we observed in the total community could be that allochthonous inputs of inactive bacteria decouple aquatic population dynamics from relative abundances.

In conclusion, we show that stabilizing biotic interactions and the ability to enter reduced metabolic life stages may play important roles in maintaining microbial diversity in nature. These processes enhance our understanding of Earth's vast microbial diversity, building on other explanations that emphasize microbial metabolic diversity (Sala et al. 2008), capacity for rapid growth (Shade et al. 2014), and micro-scale spatial structure (Vos et al. 2013). In particular, strong NFD may explain why many bacterial taxa persist at low average relative abundances (Lynch and Neufeld 2015) and dormancy (or slow growth strategies) provides an important buffer against extinction (Lennon and Jones 2011). More generally, our work demonstrates the importance of NFD in microbial systems, expanding on work from macro-organismal communities (Yenni et al. 2017; Rovere and Fox 2019), offering new explanations for the maintenance of microbial diversity.

2.6 Acknowledgements

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CHAPTER 3
DORMANCY IN METACOMMUNITIES

3.1 Abstract

Although metacommunity ecology has improved our understanding of how dispersal affects community structure and dynamics across spatial scales, it has yet to adequately account for dormancy. Dormancy is a reversible state of reduced metabolic activity that enables temporal dispersal within the metacommunity. Dormancy is also a metacommunity-level process because it can covary with spatial dispersal and affect diversity across spatial scales. We develop a framework to integrate dispersal and dormancy, focusing on the covariation they exhibit, to predict how dormancy modifies the importance of species interactions, dispersal, and historical contingencies in metacommunities. We used empirical and modeling approaches to demonstrate the utility of this framework. We examined case studies of microcrustaceans in ephemeral ponds, where dormancy underlies metacommunity dynamics, and identified constraints on the dispersal and dormancy strategies of bromeliad-dwelling invertebrates. Using simulations, we showed that dormancy can alter classic metacommunity patterns of diversity in ways that depend on dispersal-dormancy covariation and spatiotemporal environmental variability. We propose that dormancy may also facilitate evolution-mediated priority effects if locally adapted seed banks prevent colonization by more dispersal-limited species. Last, we present testable predictions for the implications of dormancy in metacommunities, some of which may fundamentally alter our understanding of metacommunity ecology.

3.2 Introduction

Metacommunity ecology provides a framework for understanding how processes on multiple spatial scales influence the assembly, structure, and dynamics of communities (Leibold et al. 2004;

This chapter has been published in the journal *The American Naturalist* (Wisnoski et al. 2019).

Holyoak et al. 2005; Leibold and Chase 2018). At the local scale, niche selection (due to abiotic constraints and species interactions) and demographic stochasticity regulate community structure (Chesson 2000b; Adler et al. 2007; Gravel et al. 2011; Vellend 2016). At the regional scale, spatial heterogeneity and dispersal control the feedbacks that arise among communities, while the diversity of species and their degree of niche differentiation reflect the biogeographical history of the regional species pool (Mittelbach and Schemske 2015; Vellend 2016). To date, the primary focus of metacommunity ecology has been on dispersal in relation to local processes, such as niche selection (e.g., species sorting and mass effects models; Cadotte 2006; Grainger and Gilbert 2016; Soininen 2016), stochasticity (e.g., neutral models; Hubbell 2001), or competitive hierarchies (e.g., patch dynamics models; Tilman 1994). However, the maturation of metacommunity ecology has demonstrated the need to move beyond idealized models like these and instead focus on a broader metacommunity state space defined by continuous gradients of dispersal, niche selection, stochasticity, and historical biogeography (Vellend 2016; Brown et al. 2017; Leibold and Chase 2018). There is also a growing need to incorporate additional ecological factors to explain discrepancies between theoretical predictions and patterns found in nature.

While metacommunity ecology has overwhelmingly focused on spatial dispersal, many species can also engage in dormancy, a reversible state of reduced metabolic activity that allows individuals to disperse through time via storage in a "seed bank" of long-lived inactive propagules (De Stasio 1990; Hairston and Kearns 2002). Dormancy is of particular relevance for metacommunity ecology because (1) it can buffer against temporarily harsh environments that could lead to local extinctions (i.e., dormancy weakens the strength of local niche selection; Lennon and Jones 2011), (2) it can covary with dispersal (Buoro and Carlson 2014), and (3) it has implications for the eco-evolutionary dynamics that influence species distributions across space and time (De Meester et al. 2016). For example, spatial and temporal patterns of diversity in metacommunities, such as colonizationextinction dynamics in a landscape, are typically explained on the basis of spatial dispersal and niche selection in response to environmental variability (e.g., disturbance and recolonization). However, similar patterns may not only be influenced by dormancy (Mahaut et al. 2018) but may

fundamentally depend on it (box 1).

Despite its potential importance for localand regionalscale processes, dormancy has yet to be adequately incorporated into metacommunity ecology (Leibold and Norberg 2004; Holt et al. 2005; Alexander et al. 2012). Here, we explore the role of dormancy in metacommunities from both ecological and evolutionary perspectives. We first review the evolutionary ecology of dispersal and dormancy as life-history strategies for coping with variable environments and emphasize that these traits are not necessarily independent (Buoro and Carlson 2014). We then consider the ecological and evolutionary implications of dormancy for community assembly, metacommunity dynamics, and species distributions in metacommunities. We also examine case studies where dormancy underlies metacommunity dynamics, create a simulation model showing that dormancy affects diversity across spatial scales, and analyze the dispersal and dormancy strategies of a large collection of taxa to show how metacommunity ecologists might incorporate dormancy into their research. We conclude with future directions to further integrate dormancy into metacommunity ecology.

3.3 The evolutionary ecology of dispersal and dormancy

Dispersal is the net movement of organisms away from their natal habitat. It minimizes the risk of local extinction, reduces kin competition, accommodates foraging strategies, and allows populations to track environmental conditions across the landscape (for recent reviews, see Ronce 2007; Cheptou et al. 2017; Cote et al. 2017). Dispersal also promotes species coexistence at the regional scale if it increases intraspecific competition relative to interspecific competition (Amarasekare 2003). For example, competition-colonization trade-offs allow inferior resource competitors to coexist in the metacommunity if they are better at colonizing recently disturbed habitats (Tilman 1994). Dispersal-mediated co-existence can be further enhanced by spatial heterogeneity. Spatial heterogeneity allows different species to be favored in different patches of the metacommunity, a crucial element of the spatial storage effect (Chesson 2000a; Shoemaker and Melbourne 2016). Spatial heterogeneity also provides the environmental context that determines whether dispersal is limiting, sufficient, or too high relative to the strength of local niche selection, which regulates the

degree to which species distributions can be explained by environmental variation alone (Leibold and Chase 2018). Although it offers many benefits, dispersal is costly; it requires time, energy, and risk, which suggests possible trade-offs with other life-history traits (Bonte et al. 2012; Stevens et al. 2012), such as dormancy.

Dormancy is a reversible state of reduced metabolic activity that has independently evolved many times across the tree of life (Guppy and Withers 1999; Evans and Dennehy 2005; Lennon and Jones 2011; Rafferty and Reina 2012). We focus on forms of dormancy that result in the production of metabolically inactive propagules that accumulate into a seed bank. The seed bank buffers against harsh environmental conditions and may contribute to the long-term maintenance of taxonomic, phylogenetic, and functional diversity (Warner and Chesson 1985; Hairston and Kearns 2002; Lennon and Jones 2011). If the environment favors different species at different times, dormancy can promote species coexistence via the temporal storage effect (Warner and Chesson 1985), such that species partition temporal niches due to the preservation of overlapping generations in the seed bank (Chesson 2000b). Dormancy may also affect the relative strength of deterministic versus stochastic eco-evolutionary processes by altering population sizes (Ellstrand and Elam 1993; Orrock and Watling 2010; Gilbert and Levine 2017; Shoemaker and Lennon 2018). In unpredictable environments, a fraction of the population could re-main dormant even when environmental conditions are favorable (i.e., bet hedging; Evans and Dennehy 2005; Childs et al. 2010; Starrfelt and Kokko 2012). As with dispersal, dormancy has costs, including delayed reproduction, losses due to burial (Hairston et al. 1995) or predation (Janzen 1971; Horst and Venable 2018), and the energetic costs of producing and maintaining dormant life stages (Finkelstein et al. 2008; Lennon and Jones 2011).

As two of the most common strategies for coping with environmental variability, dispersal and dormancy are similar in many ways (Den Boer 1968; Bohonak and Jenkins 2003). Successful spatial and temporal dispersal consists of three phases: (1) emigration, or initiation of dormancy; (2) movement, or survival through unfavorable environments; and (3) colonization, or reactivation from dormancy (Buoro and Carlson 2014). We operationally define the dispersal and dormancy

capacities of a species based on its ability to successfully complete these three phases of spatial or temporal dispersal. Species with greater capacities for dormancy may accumulate into a persistent seed bank that spans greater temporal scales (i.e., a large temporal species pool), while species that engage in short-term dormancy could occupy a transient seed bank. The collection of dispersal and dormancy traits among species in the metacommunity can then influence the types of metacommunity dynamics that arise (Fig. 3.1). Thus, relative to the spatiotemporal scales of environmental variability, some species can disperse further in time while other species can disperse further in space, setting up comparable axes that facilitate the joint investigation of dispersal and dormancy in a metacommunity context.

Despite their similarities, dispersal and dormancy can have different implications for metacommunity ecology depending on environmental variability (Levin et al. 1984; Venable and Brown 1988; Cohen and Levin 1991). For example, species with better dispersal capabilities should be favored in spatiotemporally variable landscapes with low to intermediate spatial synchrony, such that dispersal allows populations to track favorable habitats through space and time in the metacommunity (McPeek and Holt 1992). In contrast, dormancy should be favored in temporally fluctuating landscapes with high spatial synchrony (i.e., many patches experience similar conditions, reducing the effectiveness of dispersal) or when favorable habitats are spatially isolated (for a review, see Buoro and Carlson 2014). Dispersal and dormancy may also differ in their ability to maintain diversity in disturbed landscapes (McPeek and Kalisz 1998). Temporal dispersers in the seed bank may be better protected against short-term regional-scale disturbances that eliminate spatial refuges (e.g., hurricanes). Alternatively, spatial dispersers may be better protected against local-scale disturbances that outlast the range of temporal dispersal, allowing species to persist in other patches of the metacommunity. Currently, dispersal and spatial heterogeneity dominate contemporary understanding of metacommunity dynamics, but dormancy and temporal variability are analogous factors that can interactively influence diversity across space and time (Fig. 3.1).

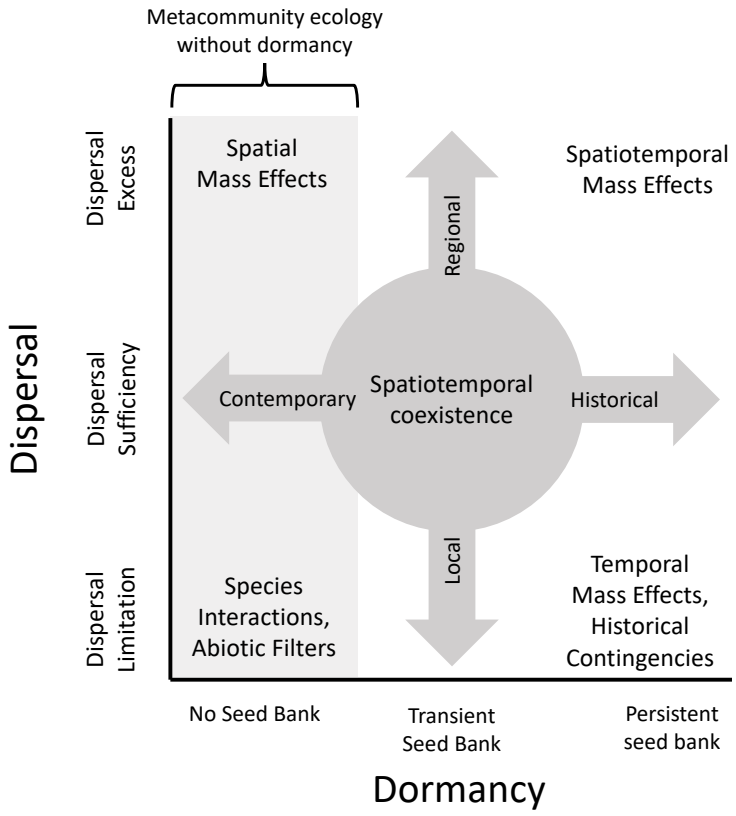

Figure 3.1: Dormancy expands the possible metacommunity dynamics to include historical factors due to the presence of a seed bank. As dispersal increases (along the vertical axis), regional factors become increasingly important for local community structure and dynamics. As dormancy increases (along the horizontal axis), propagules in the seed bank have greater temporal dispersal capacities and the potential to influence future ecological and evolutionary dynamics. In the absence of a seed bank, traditional metacommunity theory applies, leading to outcomes predicted when dispersal is limiting, sufficient, or in excess of the strength of local niche selection. Toward the lower right corner (high temporal dispersal, low spatial dispersal), historical contingencies and dispersal limitation may dominate community assembly, causing high spatial turnover relative to what would be expected based on spatial heterogeneity and dispersal alone. Increasing dispersal is likely to mitigate the historical controls from the seed bank, potentially leading to spatial and temporal homogenization, as our models indicate under positive dispersal-dormancy covariation.

3.3.1 Dispersal-dormancy covariation

The relationship between dispersal and dormancy is a key component of the life history of a species (Buoro and Carlson 2014; Rubio de Casas et al. 2015). It is often assumed that dispersal and dormancy negatively covary, consistent with the view that there is a trade-off between these life-history strategies, such that species with high capacities for dormancy have low dispersal rates and vice versa. This tradeoff is thought to exist because dormancy reduces local fitness variability and, thus, the need to disperse (Levin et al. 1984; Cohen and Levin 1987, 1991). For example, a synthesis of British seed plants indicated that species with better dispersal abilities had lower dormancy capabilities (Rees 1993). Allocation constraints could also prohibit maximal investment in traits that enhance both dormancy and dispersal, setting up the trade-off (Ehrlén and van Groenendael 1998). Additional empirical support for negative dispersal-dormancy covariation exists (Ehrlén and van Groenendael 1998; Bégin and Roff 2002), but it is not universal (Siewert and Tielbörger 2010; Buoro and Carlson 2014), suggesting that other factors may mask this trade-off.

There is also evidence that dispersal and dormancy can exhibit different relationships. Positive dispersal-dormancy covariation, where species with greater capacities for dormancy also disperse greater distances across space, is another possibility. Positive covariation could arise under a number of conditions, such as when environmental favorability changes rapidly or unpredictably in both space and time (Venable and Brown 1988; Cohen and Levin 1991; Snyder 2006; Buoro and Carlson 2014). Positive dispersal-dormancy covariation may also be due to genetic linkage or pleiotropy (Peiman and Robinson 2017), such as when traits that increase capacities for dormancy interact with traits that enhance dispersal abilities or vice versa. In this case, positive selection for dispersal or dormancy indirectly selects for the other strategy as well. For example, zooplankton that produce more durable dormant propagules make longer-lasting contributions to local seed banks, but they also disperse greater distances by better surviving ingestion by waterfowl, important dispersal vectors of freshwater invertebrates (Figuerola and Green 2002; Viana et al. 2016). Regardless of the mechanism behind dispersal-dormancy covariation, estimating dispersal and dormancy capabilities is key to capturing the full range of metacommunity dynamics (box 2).

3.4 The metacommunity ecology of dormancy

To demonstrate how covariation between dormancy and dispersal influences metacommunities, we created a simulation model (box 3, app. C.1). Our modeling demonstrates that dormancy affects the distribution of local (α), among-site (β), and regional (γ) diversity along a dispersal gradient (Fig. 3.4). In addition, our models reveal that the effects of dormancy on metacommunity diversity depend on the degree of spatiotemporal variability in the environment, species' capacities for spatial and temporal dispersal, and the type of dispersal-dormancy covariation in the metacommunity. In this section, we expand on our modeling results by discussing the potential mechanisms by which dormancy can affect three important aspects of metacommunity ecology: community assembly, community dynamics, and species distributions.

3.4.1 Community assembly

Seed banks can introduce temporal variability in the spatial scale of community assembly. This arises in part because the importance of the seed bank is greatest during the early stages of community assembly (Roxburgh et al. 2004). For example, seed banks allow weeds to rapidly colonize ephemeral crop habitats until niche selection favors more competitive species (Ryan et al. 2010; Mahaut et al. 2018). Similarly, prior to the arrival of spatial dispersers, microcrustacean seed banks in temporary wetlands can drive rapid community assembly following extended periods of desiccation (box 1; Vanschoenwinkel et al. 2010; Kneitel 2018). However, even with a local seed bank, dispersal can still play a role in the early stages of assembly. Across a 40-year successional gradient in a subalpine birch forest, dispersal played a consistently strong role in community assembly, but the importance of dormancy declined with increasing time since disturbance (Vandvik and Goldberg 2006). As a result, recently or frequently disturbed plant communities tend to have the highest compositional similarity to the seed bank, but this is not always the case (Hopfensperger 2007; Saatkamp et al. 2014). Thus, transitions from local dormancydriven assembly to regional dispersal-driven assembly appear to be common, but the implications for metacommunity dynam-

ics could depend on the frequency and spatiotemporal pattern of disturbance.

Dispersal-dormancy covariation is important for community assembly because it could determine which species colonize a site from the seed bank versus from elsewhere in the metacommunity. For example, good dispersers may also be abundant in the regional seed bank (positive covariation), and the combination of spatial and temporal dispersal by these species may contribute to the homogenization of diversity among sites (box 3). Alternatively, local seed banks may contain different species than the active or dormant species found in other patches (as might be expected with negative covariation), so that spatial and temporal dispersal events reflect different species pools. Consequently, the spatial isolation and disturbance frequency of a site may be im-portant controls on community assembly because they determine whether community assembly proceeds primarily from spatial or temporal dispersal. For example, spatial isolation plays a major role in the assembly of benthic macroinvertebrates in intermittent streams in the US Southwest because sites near perennial headwaters are colonized via spatial dispersal while sites near intermittent headwaters rely on dormancy (Bogan and Lytle 2007; Bogan et al. 2015).

3.4.2 Community dynamics

Dormancy can interact with local community dynamics in ways that may be decoupled from dispersal rates, depending on dispersal-dormancy covariation. As a result, dormancy could help explain empirical deviations from classical metacommunity predictions based on dispersal rates, niche differences, and spatial heterogeneity alone. For example, sufficient dispersal rates are thought to be necessary for species to persist in disturbance-prone landscapes (Hanski and Gilpin 1997), but seed banks can maintain local colonization-extinction dynamics in the absence of dispersal from the metacommunity if environmental conditions fluctuate on timescales that are shorter than the range of temporal dispersal by propagules in the seed bank (Mergeay et al. 2007, 2011; Ventura et al. 2014). The spatial variation in community dynamics generated by temporal dispersal could appear indistinguishable from that generated by spatial dispersal, but it would be due to purely local processes or as a result of combined spatial and temporal dispersal (Mahaut et al. 2018).

Even with strong temporal environmental tracking, reactivation from dormancy does not necessarily lead to successful reestablishment of a population. Reestablishment from the seed bank may fail due to niche preemption by similar species that have already emerged from the seed bank, introducing historical contingencies that may have stochastic elements (Fukami 2015; Schwentner and Richter 2015). Species could also emerge from the seed bank under unfavorable environmental conditions (e.g., due to stochastic reactivation or bet hedging), maintaining sink populations in the community via temporal dispersal (a temporal mass effect; Shmida and Ellner 1984; Rajaniemi et al. 2006; Mahaut et al. 2018). Other species might miss favorable opportunities for growth due to misinterpreted environmental cues or failures during the temporal dispersal process (i.e., they are "dormancy limited"; Donohue et al. 2010), which may allow competitively inferior species to occupy habitats that superior competitors fail to recolonize. Spatial variation in the stochastic or historically contingent outcomes of temporal dispersal would create mismatches between environmental conditions and community composition that current metacommunity theory might attribute to unmeasured spatial heterogeneity or dispersal. It is possible that these mismatches due to temporal dispersal could even occur in the absence of spatial heterogeneity or source-sink relationships.

3.4.3 Species distributions

Dormancy can also affect the distribution of species across the metacommunity by modifying colonization rates and patch invasibility (Gillespie et al. 2012; Gioria et al. 2012) as illustrated, for example, by the spread of exotic species by the transport of dormant propagules (e.g., in the ballast water of ships; Briski et al. 2011). Dormancy could allow colonizers that arrive during unfavorable environmental conditions to persist until conditions improve, increasing the probability of successful establishment (Gioria et al. 2012). For example, the high dispersal rate and persistent seed bank of *Acacia dealbata* may contribute to its invasiveness and expanding spatial distribution (Gibson et al. 2011). In a recent study, the seed bank density of *A. dealbata* reached more than 60,000 seeds m^{-2} in invaded plots, compared with only 9 seeds m^{-2} in uninvaded plots (Passos et al. 2017). Invasion by *Acacia* has also been shown to reduce the density of native seeds in the seed bank,

which further reinforces aboveground losses in species diversity (Gioria et al. 2014; Gioria and Pyšek 2016). The large seed banks of invasive species may even buffer the community against subsequent invasion due to rapid colonization. Thus, when coupled with high dispersal ability, dormancy may facilitate spatial homogenization not only by reducing and replacing local diversity within a site but also by facilitating the rapid spread of species throughout a metacommunity (box 3).

Dormancy can also affect the spatial distribution of species via temporal mass effects. Even if species have the ability to persist in a seed bank via dormancy, environmental conditions may not always favor establishment. For example, dormancy and dispersal maintain thermophilic bacteria in the cold Arctic Ocean, an environment where they are metabolically disfavored (Hubert et al. 2009). The ability of microorganisms to persist in unfavorable environments via dormancy could also help explain deviations in their spatial and temporal patterns of diversity from those of macroorganisms (Lennon and Jones 2011; Shade et al. 2018). In another example from an alpine lake, local seed banks enabled the recovery of a cladoceran species (*Daphnia middendorffiana*), which can grow asexually, but not a copepod species (*Hesperodiaptomus shoshone*), which relies on sexual reproduction (Sarnelle and Knapp 2004). For the copepod, finding a mate after emerging from the seed bank is rare, causing an Allee effect (Sarnelle and Knapp 2004; Kramer et al. 2008). Although temporal mass effects may explain the occasional presence of a copepod in this lake, their lack of recovery also suggests that they could be dispersal limited relative to nearby lakes. Thus, dormancy can influence the spatial distributions of species in a metacommunity, often in unanticipated ways, due to spatial and temporal processes.

3.5 Evolving metacommunities with dormancy

Dormant seed banks could further influence community assembly and metacommunity dynamics through evolutionary processes by altering the arrival of species and rates of local adaptation (Leibold et al. 2005; Urban and Skelly 2006; Loeuille and Leibold 2008; Urban et al. 2008; De Meester et al. 2016). The community monopolization hypothesis posits that local adaptation by early-

arriving species can create priority effects that prevent the establishment of laterarriving species and alter regional patterns of diversity (Urban et al. 2008; Urban and De Meester 2009; Leibold et al. 2019). Community monopolization is likely to occur when early colonizers can rapidly adapt to local conditions (e.g., due to short generation times) and when colonization events are rare and infrequent (e.g., due to spatial isolation and dispersal limitation; De Meester et al. 2016; Vanoverbeke et al. 2016). But dormant seed banks provide another mechanism of colonization that could modify the importance of community monopolization for metacommunity dynamics.

Dormancy can regulate community monopolization by shortening or lengthening the time between the arrival of maladapted colonists and the arrival of preadapted species that would drive them extinct. For example, because seed banks facilitate recolonization they could lengthen the time available for early colonists to locally adapt and monopolize the community, especially when spatial isolation contributes to dispersal limitation. However, even with high immigration seed banks can be locally adapted (De Meester et al. 2002; Falahati-Anbaran et al. 2014; Ventura et al. 2014). Seed banks also store genetic diversity that provides a source of gene flow from the past (Hairston and Kearns 2002; Vitalis et al. 2004; Lundemo et al. 2009; Rubio de Casas et al. 2015). Maladaptive gene flow from the seed bank can inhibit monopolization by slowing the response to directional selection (Templeton and Levin 1979; Hairston and De Stasio 1988; Shoemaker and Lennon 2018; Tellier 2019), a process we call the "dormancy load". Alternatively, under fluctuating selection seed banks can facilitate local adaptation by allowing different genotypes to be favored at different times (i.e., a genetic storage effect; Ellner and Hairston 1994; Hedrick 1995; Nunney 2002; Vitalis et al. 2004). Thus, high dormancy load can slow local adaptation and allow a preadapted species to interrupt community monopolization. However, if early colonizers build up genetically diverse seed banks in fluctuating patches, they are more likely to monopolize them even when environmental fluctuations occur (Loeuille and Leibold 2008).

Although we have reviewed some of the possibilities above, the role of the seed bank in community monopolization will be highly context dependent. This is because the outcome of community assembly depends on the genetic variation of populations in the seed bank relative to spatial col-

onizers, the covariation between dormancy and dispersal, colonization order, and environmental variability in relation to the emergence of genotypes and species from the seed bank.

3.6 Future directions

We have shown that dormancy can have many consequences for metacommunity ecology and evolution (Table 3.1), but there remains much more to learn about how dormancy and seed banks influence the distribution of species through space and time. In this section, we briefly highlight three research needs that would yield greater insight into the possible roles of dormancy in metacommunities.

3.6.1 Modeling studies

The difficulty of empirically measuring dispersal has led to an increased reliance on models for generating and testing new hypotheses in metacommunity ecology. Likewise, challenges associated with measuring dormancy also pose significant hurdles. Modeling studies (e.g., analytical or simulation based) can be used explore the vast parameter space of dispersal and dormancy beyond what can be accurately measured in most organisms. A key challenge will be to understand how dormancy might alter the predictions of current metacommunity theory under different collections of species (with varying dispersal-dormancy covariation), under different patterns of environmental variability (e.g., spatial and temporal autocorrelation or disturbance), and under different starting conditions or assembly histories. We developed a number of hypotheses testable with simulation models, which we believe will be worthwhile starting points for modeling studies (box 4). But even under the simplified conditions specified by our models, our results suggest that dormancy affects a fundamental property of metacommunity ecology: the distribution of diversity across spatial scales (box 3). However, more complex models would yield deeper insight into the nuanced roles of dormancy in metacommunities. For example, models could extensively explore how dormancy affects metacommunity structure through local, regional, historical, and evolutionary mechanisms that are difficult or impossible to measure empirically.

Table 3.1: Modifications to metacommunity theory with the inclusion of dormancy

Concept	Without dormancy	With dormancy
Colonization-extinction dynamics	Colonization results from spatial dispersal alone	Colonization can occur from within a patch by propagules from the past
Turnover in γ-diversity	The loss or gain of a species at the regional scale indicates that a species either became extinct regionally or the metacommunity was invaded	Species may disappear and reappear in the future as a result of long-term storage in the seed bank
Diversity-dispersal relationship	Homogenization (i.e., the erosion of β-diversity) results from high rates of contemporary dispersal	Spatial and temporal dispersal interact to homogenize the metacommunity over space and time, decoupling homogenization from contemporary dispersal rates
Community monopolization	Following a disturbance, good dispersers are more likely to monopolize a new site because they can adapt locally to new conditions before the arrival of poorer dispersers	Following a disturbance, dormant organisms may rapidly colonize from the seed bank (despite being poor dispersers), allowing them to monopolize the site before spatial dispersers arrive
Sink/fugitive populations	Species can be found in suboptimal sites because of their superior dispersal abilities	Seed bank emergence could also contribute to the maintenance of populations in unfavorable habitats
γ-diversity in variable environments	Asynchronous spatiotemporal variability can drive poor dispersers extinct in the metacommunity	Temporal dispersal can allow environmental tracking within each patch (e.g., temporal storage effect), maintaining regional diversity despite dispersal limitation
Effects of disturbance on priority effects and β-diversity	Disturbances can eliminate local priority effects, which could generate temporal variability in β-diversity	Priority effects can persist across disturbance events, which could stabilize patterns of β-diversity over time

3.6.2 Empirical studies

From the empirical perspective, it is unclear whether different taxonomic groups have characteristic patterns of dispersaldormancy covariation and whether dispersal-dormancy covariation is influenced by other traits, such as body size or dispersal mode. We have shown that invertebrate species commonly found in bromeliad plants display a wide range of dispersal and dormancy capacities (box 2), but generalizations are difficult without extensive trait measurements across diverse taxonomic groups and ecosystems. Accurate measurements of dispersal and dormancy are notoriously difficult to acquire, but estimates of these traits for co-occurring species at the metacommunity scale are invaluable. For example, identifying species differences in dispersal kernels (Sullivan et al. 2018) and dormant propagule survivorship (e.g., Frisch 2002) would be especially informative for predicting how species distributions in metacommunities relate to spatiotemporal variation in the environment. Trait data could then be used to test whether predictions derived from different dispersal and dormancy strategies correspond with patterns of diversity observed in the field. For example, multivariate statistics can quantify the degree to which community dynamics are explained by spatial, temporal, biogeographical, trait, and environmental predictors (e.g., Leibold et al. 2010; Legendre and Legendre 2012; Peres-Neto et al. 2012; Dray et al. 2014; Peres-Neto et al. 2017). Furthermore, manipulative experiments in the field or in mesocosms may be able to test fundamental predictions about the roles of dispersal and dormancy in metacommunities (e.g., those identified in box 4).

3.6.3 Adding trophic complexity

Discrepancies between empirical studies and competitionbased metacommunity theory may partly result from trophic interactions, especially when consumer movement alters spatial and temporal patterns of diversity (Haegeman and Loreau 2014; Grainger and Gilbert 2016; Leibold and Chase 2018; Guzman et al. 2019). Additional complexities may arise when considering dormancy, which can further modify trophic dynamics. For example, dormant propagules often differ in their vulnerability to predators and pathogens (Hulme 1998; Klobutcher et al. 2006; Waterkeyn et al.

2011; Horst and Venable 2018), which could affect their survival in the seed bank and temporal dispersal capabilities. At the metacommunity scale, well-dispersed predators can eliminate spatial refuges for vulnerable prey, but predator-resistant dormant stages could introduce temporal refuges that stabilize prey populations in the metacommunity. In some systems, dormancy may even be an adaptation to host-parasite interactions (Verin and Tellier 2018), suggesting dormancy may be a trait of interest in evolving metacommunities that include predation. However, dormant propagules at a high risk of consumption (e.g., Waterkeyn et al. 2011) could increase predator abundances and destabilize prey populations (of several species) at the metacommunity scale via interpatch apparent competition. In addition, predators might also have the ability to enter a dormant stage. Predator seed banks could prevent prey species from occupying certain patches by driving prey extinct on reactivation (Livingston et al. 2017). These colonization-extinction dynamics resemble but fundamentally differ from those driven by dispersal (Huffaker 1958; Hilborn 1975). Our understanding of dormancy in metacommunities would benefit greatly from (1) manipulative experiments that measure how the presence or absence of predators, seed banks, and environmental heterogeneity contribute to metacommunity dynamics and (2) modeling approaches that extensively explore how more complex food webs (including predators, omnivores, mutualists, pathogens, etc.) may regulate the relative importance of dormancy and dispersal for metacommunity structure, diversity, and stability.

3.7 Conclusions

Dormancy is a common life-history trait that can influence metacommunity structure, dynamics, and diversity. Our simulations suggest that the effects of dormancy on metacommunity diversity depend on dispersal-dormancy covariation and environmental variability, proposing a tighter integration between spatial and temporal dimensions in metacommunity ecology. Building on our models, we propose that the dispersal and dormancy capacities of species in the metacommunity modify the relative importance of local (e.g., species interactions, abiotic constraints), historical (e.g., priority effects, temporal mass effects), and regional (e.g., dispersal and spatial heterogene-

ity) factors underlying metacommunity structure. The range of potential metacommunity dynamics expands even further when we incorporate evolution (e.g., via the community monopolization hypothesis), but the outcomes are likely to be highly context dependent. Dormancy can facilitate community monopolization through rapid recolonization from the seed bank and by buffering against maladaptive gene flow, but it may also inhibit monopolization if dormancy load prevents local adaptation. Using case studies from natural metacommunities, simulation models, and an analysis of dispersal-dormancy covariation, we have demonstrated some of the implications of dormancy for metacommunities and have suggested ways to more fully incorporate dormancy into metacommunity research. While the context-dependent role of dispersal in metacommunities is now increasingly clear, our synthesis reveals that dormancy may play a similarly important role that may strongly interact with that of dispersal in ways that remain to be elucidated.

3.8 Box 1: Evidence from nature: microcrustacean metacommunities

Many species are capable of entering dormant stages that can influence their distributions across time and space. Microcrustaceans, such as cladocerans, copepods, and fairy shrimp, have a broad range of dispersal (Jenkins and Buikema 1998; Cáceres and Soluk 2002; Vanschoenwinkel et al. 2009) and dormancy (Brendonck et al. 2017; Ellegaard and Ribeiro 2018) capabilities. For example, the production of dormant ephippia in response to food limitation, crowding, or seasonality (Fig. 3.2, panel A) allows species of Daphnia to coexist at the local scale via the temporal storage effect (Cáceres 1997). Daphnia have high capacities for temporal dispersal because their ephippia can remain viable for more than a century (Cáceres 1998). Dormancy also has direct implications for zooplankton metacommunity dynamics because it enables dispersal between isolated aquatic habitats by wind, water, or animal vectors (Bohonak and Jenkins 2003; Havel and Shurin 2004). Traits related to dormant propagules, such as buoyancy, can influence dispersal-dormancy covariation (Pinceel et al. 2013). For example, floating ephippia are readily dispersed, but sinking propagules remain in the local seed bank (Ślusarczyk and Pietrzak 2008). In contrast to Daphnia, cladocera in the genus Chydorus attach their ephippia to littoral macrophytes (Fryer 1972; Frey

1986), restricting their dispersal. Thus, we can use species differences in dispersal and dormancy to make predictions for metacommunity dynamics.

The influence of seed banks on metacommunity diversity has been well documented through the study of crustaceans in temporary aquatic habitats, including wetlands and rock pools. In temporary rock pools (Fig. 3.2, panel B), seed banks maintain permanent resident species by allowing them to endure periods of desiccation, but they also facilitate wind-blown dispersal to other pools when the pools are dry (Brendonck and Riddoch 1999; Jocque et al. 2010; Brendonck et al. 2017). The importance of dormancy for among-pool dispersal demonstrates how local cues to enter dormancy can have metacommunity-wide implications. In this system, the early successional niche is available exclusively to dormant organisms, consistent with the prediction that seed banks affect diversity most strongly following disturbances. The seed bank allows early successional species to persist in the metacommunity even though they are often driven locally extinct by competitors and predators that colonize later via aerial dispersal (Vanschoenwinkel et al. 2010). Additional evidence from microcrustaceans in California vernal pools (n = 787) suggests that dormancy affects regional patterns of diversity (Kneitel 2016, 2018). Among generalists in this system, passive dispersers with the ability to enter dormancy (ostracods, cladocerans, and copepods) have much higher site occupancy (150%) than active dispersers that lack dormancy (Kneitel 2018). Together, these examples show how dormancy can influence metacommunity structure and dynamics in spatiotemporally variable landscapes.

3.9 Box 2: How to study dispersal-dormancy covariation in metacommunities

Incorporating dispersal-dormancy covariation into empirical and modeling studies is an important next step for fully integrating spatial and temporal dimensions into metacommunity ecology. Recently, a suite of 12 functional traits were measured for 852 invertebrate taxa that represent the species pool of the aquatic inhabitants of tropical tank bromeliads from Mexico to Argentina (Céréghino 2018; Céréghino et al. 2018). A full analysis showed that observed trait variation in the bromeliad invertebrates filled less than 25% of the potential trait space, suggesting that trait covari-

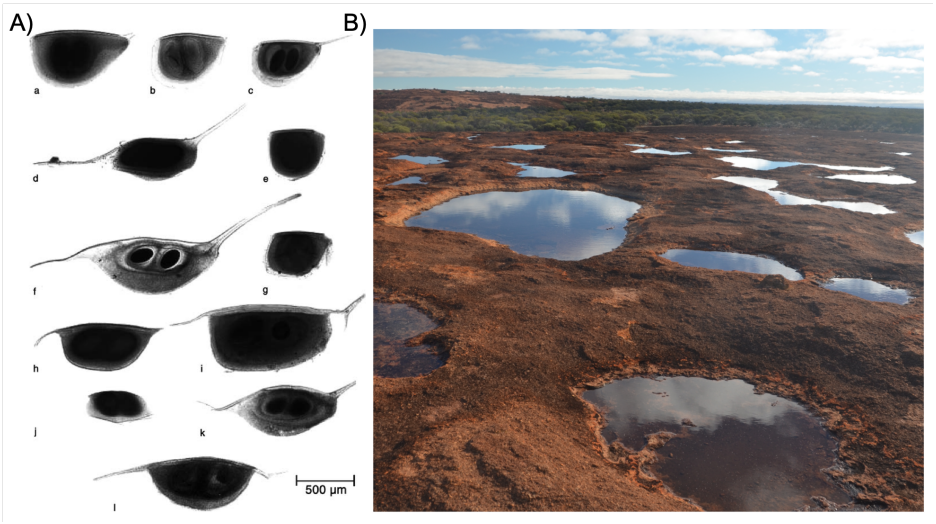

Figure 3.2: Microcrustacean dormancy is common in variable environments. A, Diversity of *Daphnia* ephippia from a survey of 41 water bodies in Kenya, where seed bank diversity was more than twice the diversity of active communities (image from Mergeay et al. 2005, reproduced with permission from Springer Nature). The high diversity lurking in the seed bank indicates the potential for dormancy to influence metacommunity trajectories in different ways depending on which species colonize the active community, the order in which they emerge from the seed bank, and the favorability of the environment they experience on reactivation. B, Temporary rock pools contain species that typically have some form of dormancy to endure extended periods of desiccation and to facilitate re- colonization from the seed bank on rewetting. Image credit: Bram Vanschoenwinkel (source: `https://insularecology.files.wordpress.com/2013/09/dsc_06291.jpg`).

ation constrains the niche space of these taxa (Céréghino et al. 2018). Bromeliad invertebrate communities are model systems for studying metacommunities because of their patchy distribution in forests, openness to colonization, and experimental tractability (Lecraw et al. 2014; Petermann et al. 2015).

Using the subset of taxa with trait measurements for both dispersal and dormancy (n = 609 taxa), we sought to identify groups of taxa with similar dispersal and dormancy strategies that may co-occur in a metacommunity. We used a fuzzy clustering algorithm (c-means) to group taxa with similar dispersal and dormancy trait values (Kaufman and Rousseeuw 1990; Maechler et al. 2018). We clustered taxa into three groups (k = 3; average silhouette width = 0.68), and used principal component analysis (PCA) on the rank-ordered trait data to visualize the location of these groups in reduced dimensions and to generate continuous descriptions of the dispersal and dormancy strategies among these taxa (Podani 2005; Borcard et al. 2018; Céréghino et al. 2018). We plot vectors showing the PCA loadings to describe the trait differences underlying cluster membership. Additional methods are available in appendix B.

We observed wide variation among taxa in their dispersal and dormancy strategies (Fig. 3.3). Notably, the first principal component describes a trade-off between passive and active dispersal ($\rho = 20.6$, $P_{Holm-adjusted} < 1 \times 10^{-9}$). The second principal component describes the dormancy capacity of each taxon. As with other trait dimensions (Céréghino et al. 2018), we found that taxa span but do not fill the dispersal-dormancy trait space, suggesting that trait covariation partially constrains dispersal and dormancy strategies. Many taxa exhibited patterns consistent with a trade-off between dispersal and dormancy: cluster 1 (lower right quadrant) includes strong passive dispersers with low dormancy capacities, cluster 2 (upper left) includes weak dispersers with high dormancy capacities, and cluster 3 (lower left) includes active dispersers with poor dormancy capacities (Fig. 3.3). However, some taxa exhibit high capacities for both dispersal and dormancy (upper right, upper left); hence, similar membership in the three clusters. More detailed information about the taxa in each cluster is available in appendix C.2.

Our analysis suggests that some species may be better at spatial dispersal while other species

are likely better at temporal dispersal but that dispersal-dormancy covariation could restrict the life-history strategies these taxa could employ. We may be able to predict their distributions in a metacommunity with knowledge of the regional species pool, the dispersal and dormancy traits of those species, and spatiotemporal variation in environmental variables by using the principal components as quantitative predictors in multivariate statistical models (e.g., the fourth-corner approach; Dray and Legendre 2008; Peres-Neto et al. 2017).

3.10 Box 3: Modeling dormancy in metacommunities

We explored the effects of dormancy in metacommunities using simulation models. A fundamental aspect of metacommunity ecology is that species diversity varies across spatial scales and can be partitioned into diversity at the local scale (α-diversity), diversity among sites (β-diversity), and diversity at the regional scale (γ-diversity). The partitioning of diversity across scales is also known to depend on the rate of dispersal in a metacommunity (Mouquet and Loreau 2003; Grainger and Gilbert 2016). Because we propose that dormancy has implications for the maintenance of diversity at the local scale and because dormancy likely covaries with dispersal, we examined the effects of dormancy on the diversity-dispersal relationship.

We modified a general metacommunity model (Shoemaker and Melbourne 2016) to include transitions in and out of a dormant seed bank. In brief, population dynamics are modeled in discrete time according to the Beverton-Holt model of population growth, dispersal is global, the metacommunity is spatially heterogeneous, dormancy occurs at a constant rate in and out of the seed bank, and dormant propagules undergo geometric decay. Because dormancy and dispersal are likely to be found in disturbed environments, we modeled random disturbance as the removal of all active individuals in a patch, following a Bernoulli distribution for each patch independently at a specified extinction rate (Shoemaker and Melbourne 2016). More details about the model and its variations can be found in appendix C.1. We partitioned diversity multiplicatively using a Hill numbers approach (order = 1, corresponding to the Shannon index of diversity), and diversity units are species equivalents (Jost 2007).

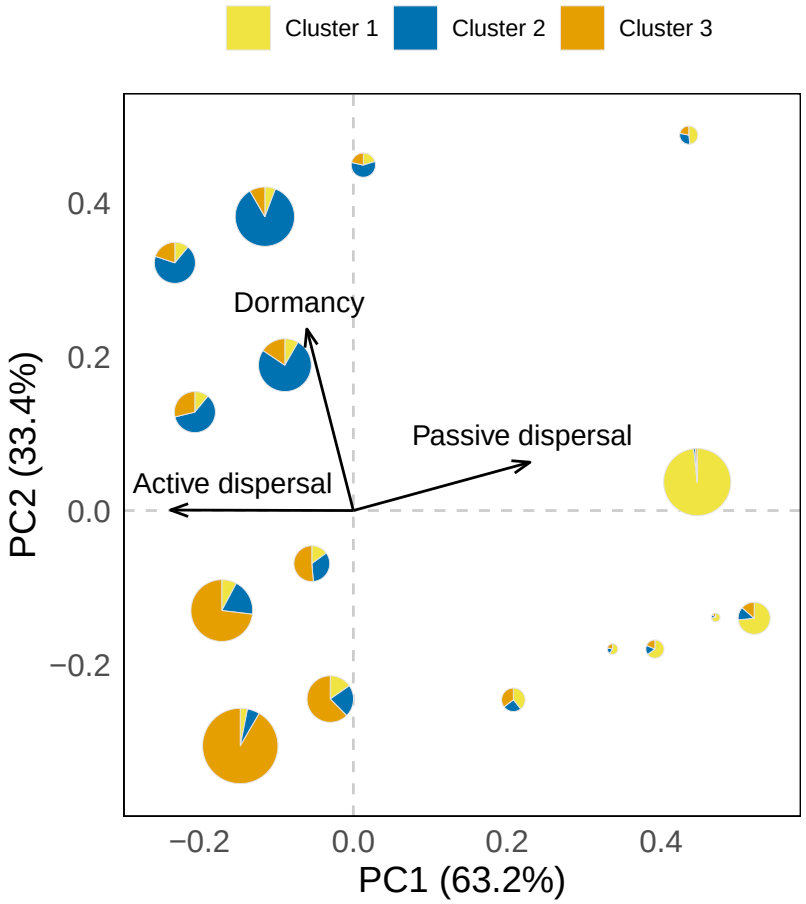

Figure 3.3: A range of dispersal and dormancy strategies were observed among aquatic invertebrate taxa found in tropical bromeliads across South America (n = 609; Céréghino 2018). The relative size of each wedge in each pie represents the proportional membership of taxa in each of the three clusters. Vectors describe the location of clusters in dispersal-dormancy trait space. Total area of the pie is proportional to the number of taxa observed with each trait combination.

Our models indicate that dormancy has substantial effects on the partitioning of diversity across scales in ways that depend on the rate of dispersal, dispersal-dormancy covariation, and environmental variability. When dispersal-dormancy covariation is negative (i.e., dormancy comes with a dispersal cost), dormancy maintains diversity when dispersal is limiting relative to disturbance rate because temporal dispersal from the seed bank allows populations to recolonize patches (Fig. 3.4). However, dormancy cannot mitigate the homogenizing effects of high dispersal rates. When there is positive dispersal-dormancy covariation, dormancy and dispersal interactively affect the dispersal rate that maximizes metacommunity diversity: dormancy maintains peak diversity at lower dispersal rates but magnifies the effects of homogenization; without dormancy, more dispersal is needed for species to keep up with the disturbance regime of the landscape (Fig. 3.4). Even in static landscapes without disturbance, where dormancy is not expected to be evolutionarily favored, seed banks can maintain higher a-diversity at lower dispersal rates and amplify the homogenizing effects of dispersal under positive dispersal-dormancy covariation (Fig. C.1).

Although by no means comprehensive, our simulations illustrate three important features of biodiversity in metacommunities: (1) dormancy alters the distribution of diversity across spatial scales, (2) these effects can depend strongly on the nature of spatiotemporal environmental variation, and (3) these effects interact with dispersal in ways that depend on the nature of dispersal-dormancy covariation.

3.11 Box 4: Testable predictions about dormancy in metacommunity ecology

- Large-scale, spatially autocorrelated disturbances will decrease β-diversity and increase the abundance of temporal dispersers; small-scale, spatially asynchronous disturbances will increase β-diversity and favor spatial and temporal dispersers.
- Spatially isolated patches will be more affected by priority effects during community assembly due to a greater role of temporal than spatial dispersal.
- Species with high capacities for dormancy and dispersal will occupy more sites in the meta-

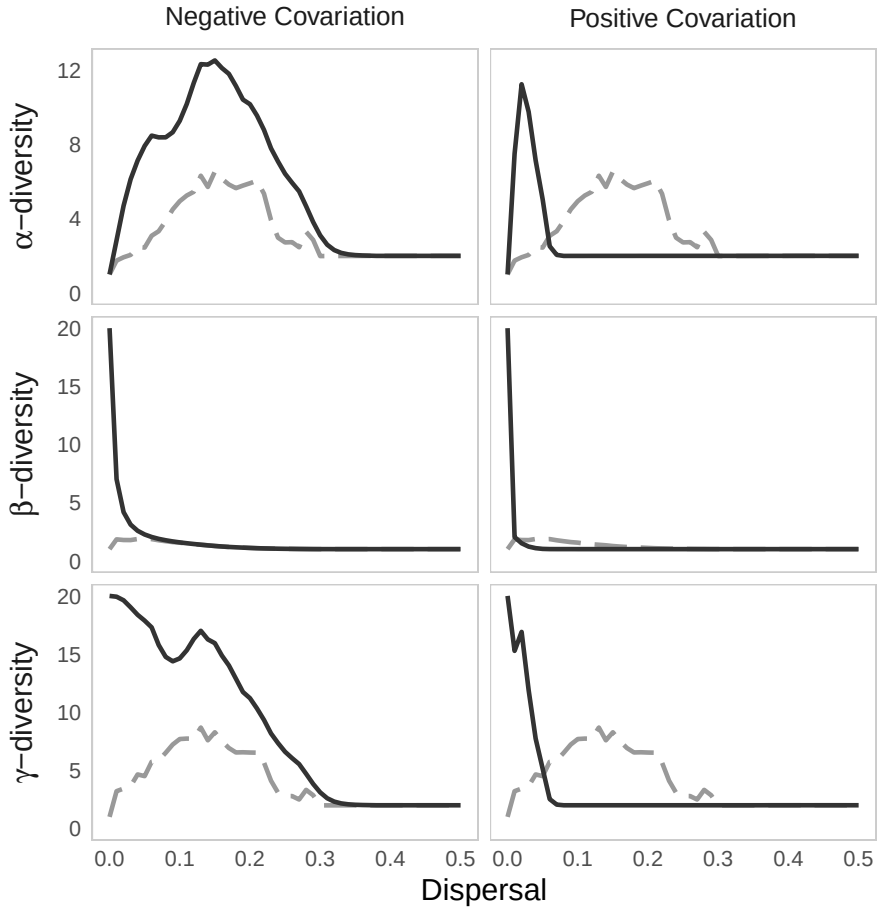

Figure 3.4: Dispersal-diversity relationships with (dark solid line) and without (dashed light line) dormancy in an environment subject to local disturbance, commonly associated with dispersal and dormancy strategies. Dormancy maintains higher α- and γ-diversity under both negative and positive dispersal-dormancy covariation. With negative covariation (i.e., a trade-off), dormancy maintains higher α- and γ-diversity, especially at lower dispersal rates, and maintains β-diversity under dispersal limitation (i.e., at very low dispersal rates). However, dormancy cannot protect against homogenization (regional diversity decreases with increasing dispersal, regardless of dormancy). With positive dispersal-dormancy covariation, dormancy lowers the dispersal rate that maximizes α-, β-, and γ-diversity; increases maximum α- and γ-diversity; and also increases the homogenizing effects of dispersal. The metacommunity with dormancy is homogenized (e.g., one species dominates) at dispersal rates that were potentially limiting in the absence of dormancy.

community and have larger species ranges than species that exhibit a trade-off between dormancy and dispersal or that lack dormancy altogether.

- In directionally changing environments, dormancy will inhibit community monopolization by imposing high dormancy load; in fluctuating environments, dormancy will facilitate monopolization via genetic storage effects.

- Species-area relationships (SARs) will have higher intercepts and steeper slopes (with negative dispersal-dormancy covariation) or shallower slopes (with positive dispersal-dormancy covariation) than SARs without dormancy.

- Species with high capacities for dormancy are likely to be dispersal limited under negative dispersal-dormancy covariation and at risk of spatial mass effects under positive dispersal-dormancy covariation, creating mismatches between species composition and environmental conditions.

- In trophic metacommunities, when dormant propagules are vulnerable to predation, dormancy may lead to apparent competition, but when dormant propagules are resistant to predation, dormancy could provide a refuge that maintains prey diversity.

- In metacommunities with frequent local disturbances but high spatial isolation between patches, dormancy may be more important for community dynamics and species distributions than dispersal when species exhibit a trade-off between dispersal and dormancy.

- In spatiotemporally fluctuating environments, when local fluctuations occur on longer timescales than the temporal dispersal range of species in the metacommunity, dormancy is less important than dispersal for maintaining diversity under negative dispersal-dormancy covariation (because individuals are lost to the seed bank); under positive dispersal-dormancy covariation, dormancy could help maintain diversity at low spatial dispersal rates.

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3.13 Publication notes

This chapter has been published in the journal *The American Naturalist* as a Synthesis article (Wisnoski et al. 2019). Supplemental information can be found in Appendix C.

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CHAPTER 4
METABOLIC INSIGHT INTO BACTERIAL COMMUNITY ASSEMBLY ACROSS ECOSYSTEM BOUNDARIES

4.1 Abstract

The movement of organisms across habitat boundaries has important consequences for populations, communities, and ecosystems. However, because most species are not well adapted to all habitat types, dispersal into suboptimal habitats could induce physiological changes associated with persistence strategies that influence community assembly. For example, high rates of cross-boundary dispersal are thought to maintain sink populations of terrestrial bacteria in aquatic habitats, but these bacteria may also persist by lowering their metabolic activity, introducing metabolic heterogeneity that buffers the population against species sorting. To differentiate between these assembly processes, we analyzed bacterial composition along a hydrological flow path from terrestrial soils through an aquatic reservoir by sequencing the active and total (active + inactive) portions of the community. When metabolic heterogeneity was ignored, our data were consistent with views that cross-boundary dispersal is important for structuring aquatic bacterial communities. In contrast, we found evidence for strong species sorting in the active portion of the aquatic community, suggesting that dispersal may have a weaker effect than persistence strategies on aquatic community assembly. By accounting for metabolic heterogeneity in complex communities, our findings clarify the roles of local- and regional-scale assembly processes in terrestrial-aquatic meta-ecosystems.

4.2 Introduction

The movement of material and energy across habitat boundaries is important for the structure and function of recipient ecosystems (Polis et al. 2004; Gounand, Harvey, et al. 2018). These spatial

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resource subsidies can stabilize population dynamics, alter food web structure, and modify biogeochemical cycles (Polis et al. 2004; Massol et al. 2011). However, in complex landscapes linked by spatial fluxes of resources and organisms, the process of community assembly remains less clear (Gounand, Harvey, et al. 2018). Meta-ecosystem theory predicts that poorly adapted species dispersed across ecosystem boundaries will be eliminated from the recipient habitat via species sorting (Massol et al. 2017; Gounand, Harvey, et al. 2018), unless resource flows sufficiently homogenize the landscape (Gravel et al. 2010). However, if generalist species are capable of tolerating a range of environmental conditions, then cross-boundary dispersal could affect community assembly in recipient habitats (Haegeman and Loreau 2014).

Habitats at the terrestrial-freshwater interface are ideal for addressing questions about meta-ecosystem ecology (Gounand, Little, et al. 2018). Terrestrial ecosystems export large quantities of organic matter that support aquatic food webs, often through bacterial pathways (Berggren et al. 2010). Furthermore, many of the bacteria responsible for processing allochthonous subsidies in aquatic habitats may be derived from terrestrial ecosystems via coupled transport with resource flows (Ruiz-González, Niño-García, Lapierre, et al. 2015). For example, in some north temperate lakes, it is estimated that nearly 1020 bacterial cells are transported annually from terrestrial to aquatic ecosystems (Bergström and Jansson 2000). These high immigration rates should influence the composition and activity of bacterial assemblages via metacommunity processes, such as source-sink dynamics or mass effects that overcome species sorting (Crump et al. 2012; Lindström and Langenheder 2012; Ruiz-González, Niño-García, and del Giorgio 2015).

Although cross-boundary flows have been well documented, the fate of terrestrial-derived bacteria in aquatic ecosystems remains unclear (Langenheder and Lindström 2019). In part, this may be because both dispersal- and niche-based perspectives overlook the range of metabolic states within microbial communities. In nature, some microorganisms may respond to favorable environmental conditions via rapid growth, while others face challenging conditions that limit or prevent growth (Lever et al. 2015)). Many bacteria have evolved persistence strategies (e.g., spores, cysts, resting stages, slow growth) that buffer against harsh environmental transitions, such as those encountered

when dispersed along terrestrial-aquatic flow paths (Barcina et al. 1997; Lennon and Jones 2011). By weakening the strength of species sorting, these persistence strategies may increase the apparent similarity between terrestrial and aquatic bacterial communities (Nemergut et al. 2013; Wisnoski et al. 2019; Locey et al. 2020), especially when techniques are used that lend equal weight to active, slow growing, and dormant bacteria (e.g., DNA-based methods). As a result, the importance of terrestrial-derived bacteria in aquatic community assembly may not be fully understood when inferred from diversity patterns that do not explicitly consider the metabolic heterogeneity that exists within bacterial communities.

In this study, we explored microbial community assembly along a hydrological flow path of a small reservoir. In this type of system, inputs from the terrestrial landscape occur upstream in the riverine zone, directional surface flow orients the passive dispersal of bacteria through the lacustrine zone, and emigration occurs over the impoundment (Fig. 4.1; Thornton et al. 1990). We hypothesized that dispersal maintains terrestrial-derived bacteria in the reservoir, promoting local (α) diversity and homogenizing among-site (β) diversity at the terrestrial-aquatic interface, but that these taxa may not be metabolically active. Due to species sorting, we hypothesized that only a subset of the immigrating terrestrial bacteria become metabolically active members of the aquatic community.

4.3 Methods

4.3.1 Study system

University Lake is a meso-eutrophic reservoir located in Griffy Woods, Bloomington, Indiana, USA (39.189, -86.503) (Fig. 4.1). Created in 1911, the 3.2 ha impoundment has an operating volume of 150,000 m^3. With a maximum depth of 10 m, University Lake is fed by three streams that drain mature oak-beech-maple forest. The underlying geology is Harrodsburg limestone on ridgetops and Borden siltstone/shale in valleys. The thin unglaciated soils surrounding the reservoir are Brownstown-Gilwood silt loams.

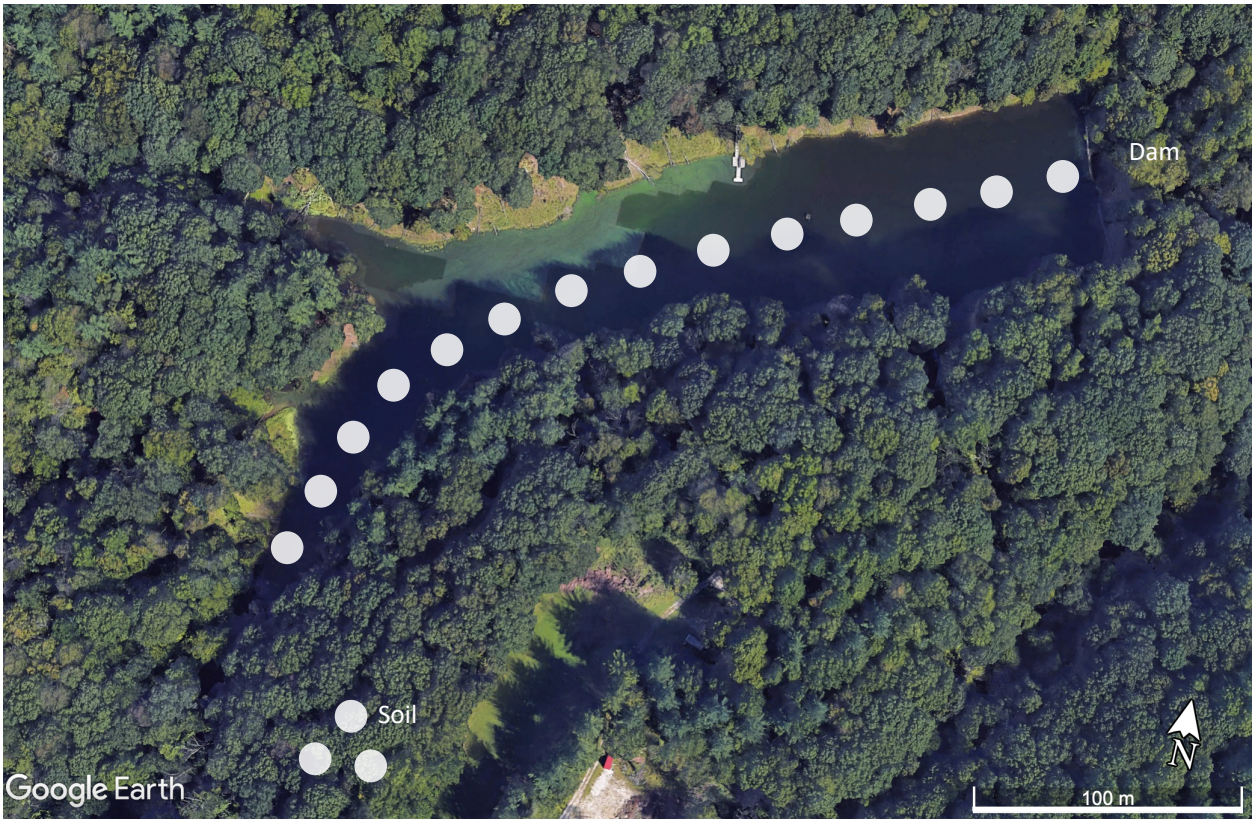

Figure 4.1: University Lake, a reservoir located on the Indiana University Research and Teaching Preserve in Bloomington, Indiana, USA. Points indicate sampling locations along the terrestrial-aquatic transect, from upstream soils, through the stream inlet, across the lacustrine zone, and over the dam. Image source: Google Earth.

4.3.2 Bacterial community structure

We collected surface-water samples along a longitudinal transect through University Lake in July 2013, filtering epilimnetic biomass from 200 mL of water onto 0.2 µm Supor Filters (47 mm diameter, Pall). We characterized composition of the active and total portions of the bacterial communities by sequencing 16S rRNA genes (DNA) and transcripts (RNA), respectively. While sequences recovered from the DNA pool can come from active or inactive individuals, sequences from the RNA pool are commonly used to make inferences about active microorganisms given that rRNA transcripts have short half-lives and that ribosomes are required by cells for protein synthesis (Molin and Givskov 1999; Bowsher et al. 2019; Steiner et al. 2019; Locey et al. 2020). Sequences were processed in mothur (v. 1.41.1 Schloss et al. 2009) and 97% similar operational taxonomic units (OTUs) were created using the OptiClust algorithm (Westcott and Schloss 2017). See Appendix D for detailed methods.

4.3.3 Quantifying patterns of diversity along the flow path

We analyzed within sample (α) and among sample (β) diversity along the flow path. We estimated α-diversity using rarefaction with the 'iNEXT' R package (Hsieh et al. 2016), following singleton-correction for sequence data (Chiu and Chao 2016). We used Hill numbers (${}^qD$) for a given order, q, to weigh common and rare species using the equation

$$ {}^qD = \left(\sum_{i=1}^{S} p_i^q \right)^{\frac{1}{1-q}} $$

where p_i is the relative abundance of species $i = 1 \ldots S$. The value ${}^qD$ is the number of equally abundant species that would yield the observed value of a diversity metric, such as richness ($q = 0$), Shannon's index ($q = 1$), or Simpson's index ($q = 2$), in each aquatic sample. When different values of q are plugged into the equation for ${}^qD$, Hill numbers at higher orders (q) increasingly reflect the most common species because larger exponents reduce the influence of rare taxa in the metric. We measured β-diversity between soil and aquatic samples as the average percent similarity

(1 – Bray-Curtis) of each aquatic sample to the three soil samples using the 'vegan' package in R (Oksanen et al. 2019). To detect molecule-specific trends in α- or β-diversity along the flow-path, we used multiple regression. With aquatic α- or β-diversity as the response variable, we tested for the effects of molecule type (treating RNA vs. DNA as a categorical variable) and flow-path distance (a continuous variable in meters) on diversity. We included an interaction term to detect differences in slopes between DNA and RNA samples along the flow path.

We also analyzed taxon-level trends along the flow path. To make inferences about species sorting on terrestrial-derived bacteria (defined as the OTUs detected in soil samples), we measured changes in their relative abundances in the aquatic DNA and RNA pools. We assumed that terrestrial taxa that were disfavored in the aquatic habitat were either never detected in the active aquatic community (i.e., they were detected in the DNA, but not RNA, pool), or they became rarer in the active aquatic community along the flow path. In contrast, we assumed taxa that were favored in aquatic sites became more common along the flow path. If we detected a terrestrial OTU in at least 75% of the aquatic RNA samples, we inferred that the taxon was metabolically active in the aquatic community, but results were robust to different thresholds (Appendix D: Fig. D.4).

Furthermore, to determine whether aquatic samples were nested subsets of the soil samples (e.g., due to mass effects or species sorting favoring habitat generalists) or exhibited compositional turnover due to the gain and loss of OTUs (e.g., due to species sorting favoring habitat specialists), we partitioned β-diversity into its nestedness and turnover components from the Sørensen family of metrics (Baselga 2010) and classified OTUs based on their habitat specificity. All statistical analyses were conducted in R (v. 3.5.2, R Core Team 2018).

4.4 Results

Patterns of bacterial diversity along the flow path were strongly influenced by metabolic heterogeneity (Fig. 4.2A, $R^2 = 0.83$, $p < 0.001$), as shown by significant differences in slope and intercept of the multiple regression model (Table 4.1). In the total aquatic bacterial community (DNA), richness was highest near the terrestrial-aquatic interface and declined toward the dam. In

Table 4.1: Output from multiple regression models. Model coefficients are shown for active and total α-diversity along the transect examined at different levels of q, representing equal weighting of rare and common taxa ($q = 0$), proportional weighting ($q = 1$), and biased weighting toward common taxa ($q = 2$). In these models, intercepts represent estimates of total diversity at each order near the terrestrial-aquatic interface, with the RNA term capturing the reduced diversity in the active subset. With increasing order, the distance × RNA interaction becomes weaker, signifying that diversity decays at similar rates in the active and total communities as common taxa are increasingly weighted.

Order (q)	Diversity	Term	Estimate	Std. Error	t-Statistic	p-value
0	Richness	Intercept	1497	100.6	14.88	$< 10^{-4}$
0	Richness	Distance	-3.176	0.4976	-6.381	$< 10^{-4}$
0	Richness	RNA	-1170	142.3	-8.222	$< 10^{-4}$
0	Richness	Distance × RNA	2.985	.7003	4.263	0.0003
1	Richness	Intercept	153.7	19.41	7.921	$< 10^{-4}$
1	Richness	Distance	-0.2941	0.096	-3.062	0.0053
1	Richness	RNA	-123.9	27.46	-4.513	0.0001
1	Richness	Distance × RNA	0.2457	0.1352	1.818	0.0815
2	Richness	Intercept	55.44	6.47	8.57	$< 10^{-4}$
2	Richness	Distance	-0.0783	0.032	-2.446	0.0221
2	Richness	RNA	-36.78	9.151	-4.019	0.0005
2	Richness	Distance × RNA	0.0402	0.045	0.8918	0.3813

comparison, the active (RNA) aquatic richness was lower and less variable along the transect. Differences in α-diversity between active and total portions of the community were highest near the terrestrial-aquatic interface (e.g., subtracting the RNA term (1170) from the intercept (1497 OTUs) of the $q = 0$ model indicates there were 78% fewer taxa in the active subset near the terrestrial-aquatic interface; Table 4.1). Across different orders of Hill numbers, diversity differences were greatest when rare and common taxa were equally weighted ($q = 0$), as might be expected if immigrant or dormant taxa were rare. When dominant taxa were weighted more heavily ($q = 1, 2$), the active portion of the community still had lower diversity overall (significant RNA terms), but differences in the decay of diversity became less distinguishable between the two portions of the community as stronger emphasis was placed on the dominant taxa (distance × RNA interaction; Table 4.1).

Metabolic heterogeneity also had strong effects on β-diversity (Fig. 4.2B). Similarity between terrestrial and aquatic samples was highest near the terrestrial-aquatic interface and decreased to-

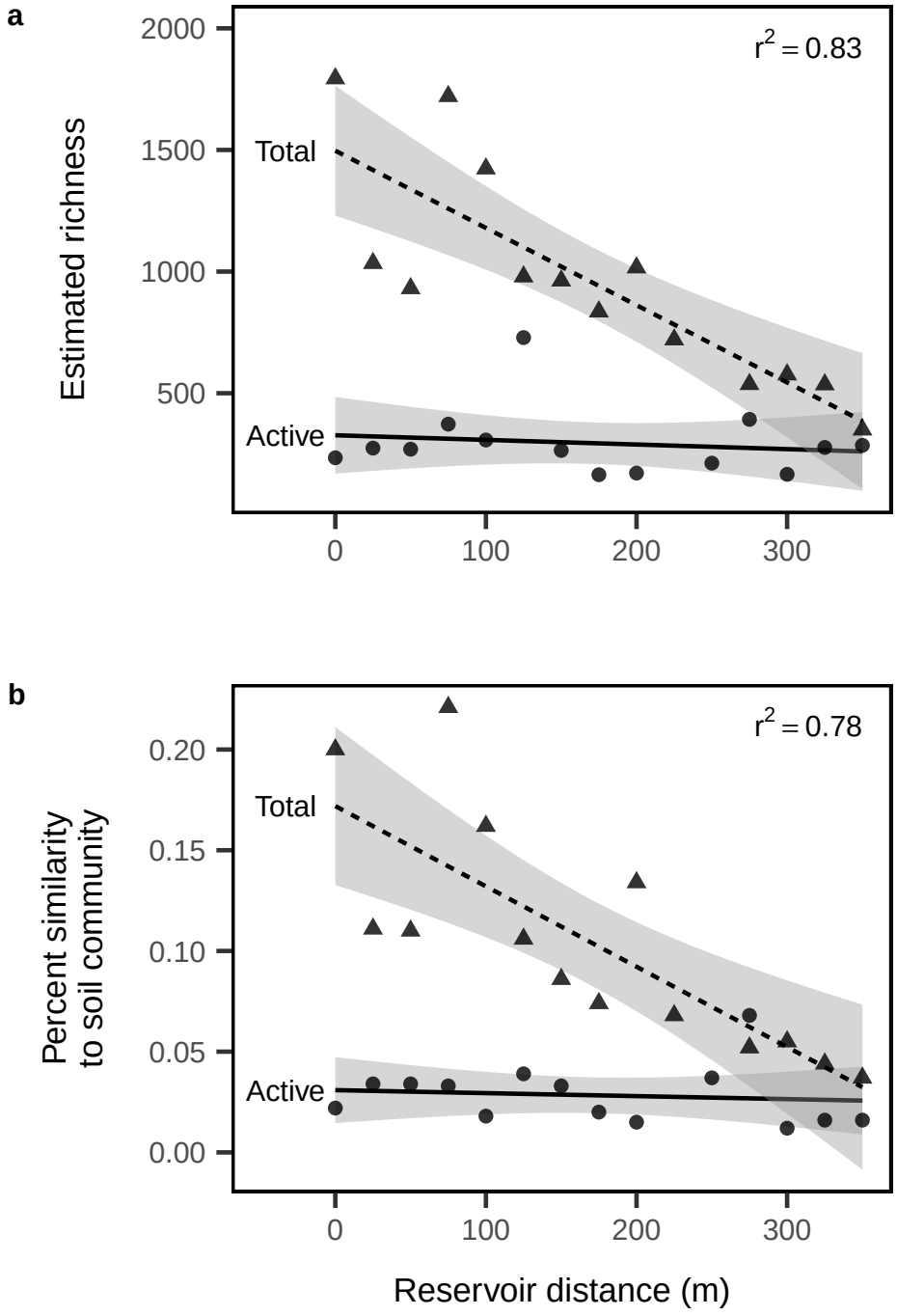

Figure 4.2: Terrestrial influence on aquatic microbial diversity. (a) Estimated alpha diversity (richness, ${}^1D$) in the active (light gray circles) and total (dark gray triangles) aquatic communities along the reservoir transect. (b) The average percent similarity to the soil samples for active and total aquatic communities declines with distance away from the terrestrial-aquatic interface (0 m).

ward the dam ($R^2 = 0.78$, $p < 0.001$). However, maximum similarity to soils and the rate of decay in similarity differed between the total and active portion of the community. Near the stream inlet, similarity to soils was > 5-fold higher in the total community than in the active portion (Intercept $= 0.172 \pm 0.014$ SE, $\beta_{RNA} = -0.141 \pm 0.020$ SE), and similarity to soils declined linearly toward the dam ($\beta_{distance} = -4.0 \times 10^{-4} \pm 6.83 \times 10^{-5}$ SE, $\beta_{distance \times RNA} = 3.9{\times}10^{-4}{\pm}9.61 \times 10^{-5}$ SE). In contrast, the active portion remained dissimilar to terrestrial soils along the entire transect (Fig. 4.2B). These patterns of β-diversity were not purely driven by nestedness, as both the active portion and the total aquatic community exhibited turnover relative to soil samples (Appendix D: Fig. D.2), and 71% of the active aquatic OTUs were not detected in the soil samples (Fig. D.3).

We detected a small number of habitat generalists (defined as OTUs present both in soil samples and in the active portion of the aquatic community), but the majority of terrestrial soil taxa did not appear to colonize the aquatic community. Most taxa present in both soil and aquatic communities were never detected in any active aquatic sample ($\sim 82\%$ of taxa remained inactive), and these inactive taxa accounted for roughly 4.5% of all reads in the total reservoir community. The richness of these taxa declined exponentially (first-order decay, $k = 2.57 \times 10^{-3} \pm 3.6 \times 10^{-4}$ SE, $r^2 = 0.81$, $p < 0.001$) with distance from the stream inlet (Fig. 4.3A). However, 13% of taxa present in soils were detected at least once in the active aquatic community. Of the soil-derived taxa detected in at least 75% of active aquatic samples, 18 declined along the transect, but 11 were maintained at high relative abundances in the active aquatic community (Fig. 4.3B; see Appendix D: Tables D.1-D.2 for list of taxa).

4.5 Discussion

Our results support the hypothesis that the importance of dispersal for community assembly across ecosystem boundaries depends on the metabolic activity of dispersers in the meta-ecosystem. Along a terrestrial-aquatic flow path, the influence of terrestrial bacteria on aquatic bacterial α- and β-diversity was highest near the terrestrial-aquatic interface. This pattern, consistent with terrestrial immigration playing an important role in aquatic community assembly (i.e., mass effects), was

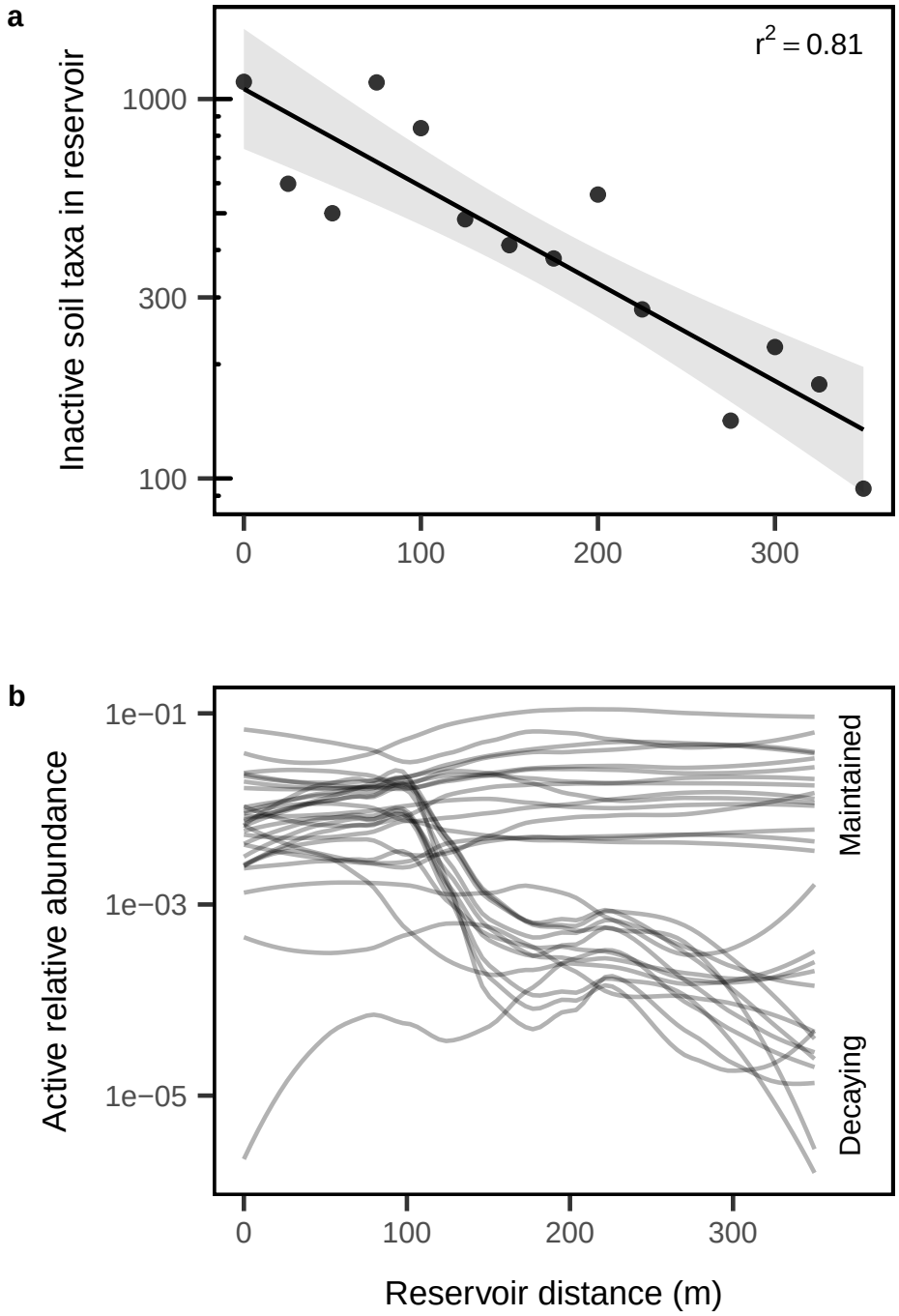

Figure 4.3: Fate of terrestrial-derived taxa in the reservoir. (a) Number of taxa detected in soils but never detected in active aquatic samples declines exponentially away from the terrestrial-aquatic interface with a first-order decay constant $k = 2.57 \times 10^{-3}$. Note the y-axis is on a logarithmic scale. (b) Taxa detected in at least 75% of active aquatic samples either decay in abundance along the transect or are maintained. We used local polynomial regression (LOESS) to visualize relative abundances for each OTU along the transect.

weaker in the active portion of the aquatic community than the total aquatic community. Specifically, both α-diversity and similarity to soils were substantially lower in the metabolically active portion of the aquatic community (Table 4.1; Fig. 4.2), suggesting a hidden role for species sorting in the aquatic habitat that was only apparent when incorporating metabolic information. In fact, most terrestrial-derived taxa were not detected in the active aquatic community and decayed exponentially away from the terrestrial-aquatic interface (Fig. 4.3). Altogether, our findings are consistent with the hypotheses that most terrestrial-derived taxa fail to colonize aquatic habitats and that only a small number of habitat generalists may be able to colonize aquatic environments from nearby terrestrial landscapes. Our study also highlights the utility of incorporating information on metabolic heterogeneity to gain insight into the structure and dynamics of spatially heterogeneous metacommunities and meta-ecosystems.

4.5.1 Metabolic heterogeneity informs aquatic community assembly

Inferring community assembly processes from diversity patterns is challenging because species can be present in a habitat for reasons other than habitat suitability (e.g., high dispersal, persistence traits). Accounting for metabolic heterogeneity helps distinguish favorable from suboptimal habitats by detecting the responses of actively growing organisms (e.g., Muscarella et al. 2016), providing insight into the fate and potential functions of dispersers in recipient ecosystems. The frequent detection of terrestrial bacteria in aquatic ecosystems has led to the view that dispersal is a dominant process structuring aquatic diversity, but our results suggest that local aquatic environments still impose harsh biotic or abiotic filters on the metabolically active subset of the aquatic community (Fig. 4.2). Thus, the strength of species sorting on terrestrial-derived bacteria in aquatic habitats may increase with metabolic activity levels of cross-boundary dispersers.

4.5.2 Exponential decay of soil-derived bacteria in aquatic ecosystems

Dispersing across an ecosystem boundary is likely a harsh transition for many bacteria (Monard et al. 2016). Although most active aquatic taxa were also detected in nearby soils, only a minority

of taxa present in soils were common in the active aquatic community (Fig. 4.3). The exponential decay of metabolically inactive terrestrial taxa away from the terrestrial-aquatic interface also resembles diversity declines near river margins (Power et al. 2004). This exponential loss could be due to physical factors (e.g., settling or volumetric dilution) or biotic interactions (e.g., consumption, competition, or lysis following reactivation) that are not offset by reproduction. While our study captured a snapshot in time, if these inactive organisms remain in the system with the potential to reactivate, they could influence community dynamics if environmental conditions change in their favor. Future studies that differentiate activities at a finer resolution (e.g., slow growing, dormant with the potential to reactivate, or even dead) (Carini et al. 2017; Lennon et al. 2018) could further illuminate the fate of cross-boundary dispersers in meta-ecosystems. In general, the exponential decay suggests that terrestrial influences on aquatic bacterial diversity may be localized near ecosystem boundaries.

Nevertheless, a subset of taxa detected in soils were active in the aquatic community. Some became less common along the transect, which could reflect sorting along a riverine-to-lacustrine environmental gradient, or a reduction in mass effects (Fig. 4.3B). These decaying taxa included representatives from the Actinobacteria (*Arthrobacter*, *Micrococcus*, *Solirubrobacter*), Bacteroidetes (*Flavobacterium*, *Pedobacter*), and Proteobacteria (α: *Bradyrhizobium*, *Sphingomonas*; β: *Duganella*, *Comamonas*; and γ: *Pseudomonas* sp.), some of which are abundant and ubiquitous in soils (Delgado-Baquerizo et al. 2018). In contrast, taxa maintained in the active aquatic community may have wide niche breadths allowing them to be habitat generalists, or they may be of aquatic origin (e.g., dispersed by floods, animals, or wind, but our soil sampling locations were chosen to minimize this possibility). These potential habitat generalists included taxa belonging to the Actinomycetales, Bacteroidetes (order Sphingobacteriales), Proteobacteria (α: order Rhizobiales, β: family Comamonadaceae, γ: *Acinetobacter*), and Verrucomicrobia (class Spartobacteria). In sum, most terrestrial-derived bacteria may possess persistence strategies that allow them to persist on the periphery of aquatic ecosystems, but habitat generalists that cross ecosystem boundaries could influence aquatic bacterial community assembly.

4.5.3 Metabolic heterogeneity in metacommunities and meta-ecosystems

Our work provides empirical evidence that accounting for metabolic heterogeneity may improve our understanding of metacommunity and meta-ecosystem processes (Massol et al. 2017; Wisnoski et al. 2019). Cross-boundary dispersal can expose organisms to harsh environmental conditions, against which they may be buffered through metabolic flexibility (e.g., slow growth, dormancy). While generalists may be able to colonize a range of habitat types in meta-ecosystems (Haegeman and Loreau 2014), specialists that disperse across ecosystem boundaries may require coupling with resource subsidies or persistence strategies that buffer against suboptimal conditions. Metabolically explicit community assembly also has implications for ecosystem functioning in a spatial context. While high dispersal is predicted to impede ecosystem functioning by creating species-environment mismatches (Leibold et al. 2017), these effects may be reduced if dispersers are metabolically inactive and minimally affect recipient communities. Thus, metabolic heterogeneity may be an important link for understanding the relationships between individuals, communities, and ecosystems across spatial scales.

4.6 Acknowledgements

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4.7 Publication notes

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CONCLUSION

In this dissertation, I have explored the assembly, structure, and dynamics of ecological communities using empirical studies and simulation models. In particular, my work has demonstrated the importance of dispersal and dormancy in freshwater bacterial communities and in metacommunities more generally, which I expand on here.

Dispersal

Using empirical data from stream and lake bacterial communities, my work has shown that dispersal is a key process influencing bacterial diversity in nature. In Chapter 1, I showed that the importance of dispersal-based community assembly processes in dendritic networks is dependent on habitat and spatial scale. In dendritic metacommunities, the role of dispersal is hypothesized to vary with network position, such that local environmental factors are more important in headwaters and dispersal-driven assembly increases downstream due to spillover from upstream (Brown et al. 2011; Carrara et al. 2012; Altermatt 2013). Unlike the macroorganisms for which this hypothesis was developed (Brown and Swan 2010; Schmera et al. 2018; Henriques-Silva et al. 2019), microbial dispersal through the network may be entirely passive and guided by the downstream direction of stream channel flow. In addition, microorganisms are not necessarily confined to either aquatic or terrestrial environments and may be readily dispersed across the terrestrial-aquatic interface. For example, dispersal from terrestrial ecosystems has been shown to influence headwater bacterial communities due to mass effects, but species sorting driven by local environmental conditions becomes increasingly important as bacteria drift downstream (Read et al. 2015; Ruiz-González, Niño-García, and del Giorgio 2015; Savio et al. 2015). While many insights about the role of dispersal have emerged from patterns of bacterioplankton, studies of benthic habitats have detected important roles for environmental factors that regulate species sorting (Fierer et al. 2007; Lear et al. 2013; Battin et al. 2016). My work builds on these studies by comparing spatial patterns

of community assembly in planktonic and benthic habitats of a large stream network. In particular, Chapter 1 shows that assembly depends on vertical habitat structure, network position, and spatial scale, building up to a revised conceptual framework for studying microbial metacommunities in streams focused on multi-layer dendritic networks.

Dormancy

My dissertation has also shown that dormancy can play a role in bacterial communities by contributing to the maintenance of diversity over time. In Chapter 2, I empirically demonstrated that bacterial diversity in a temperate lake may be maintained by stabilizing biotic interactions and the ability of bacteria to enter reversible states of dormancy. These factors allow bacterial populations to recover from rarity, stabilizing community dynamics and maintaining diversity, particularly during harsh winter conditions. This chapter strengthens our understanding of the processes that maintain high diversity found in bacterial communities (Jones and Lennon 2010; Thompson et al. 2017), pointing to a key role for stabilizing biotic interactions that allow the large number of rare taxa to stably coexist. Results from this chapter are also consistent with coexistence via storage effects (Chesson 2000b), including our evidence for: (1) taxon-specific responses to environmental variability via temporal niche partitioning; (2) covariance between the strength of intraspecific competition and environmental favorability, as seen from negative frequency dependent growth that suggests population dynamics are limited by the increase of conspecifics during favored conditions; and (3) buffered population growth demonstrated by the increased diversity detected in the seed bank, especially during unfavorable conditions. My work on this topic builds on our understanding of the role of dormancy in microbial communities gained from snapshots in time (Jones and Lennon 2010; Meyer et al. 2018; Locey et al. 2020), and demonstrates possible roles of microbial dormancy for maintaining diversity through time.

Joint effects of dispersal and dormancy

Dispersal and dormancy are not independent of one another. Indeed, dormancy may enable greater dispersal probabilities for small, passively dispersed organisms as they traverse unfavorable environments (Locey 2010; De Meester 2011; Nemergut et al. 2013). Alternatively, as long-lived dormant propagules accumulate into a resting bank, they may be limited in their dispersal capabilities due to individual-level trade-offs (Cohen and Levin 1987; Buoro and Carlson 2014). Thus, dispersal and dormancy can covary, either positively or negatively, which may have implications for the distribution and dynamics of biodiversity. In Chapter 3, I incorporated these ideas into metacommunity ecology by discussing case studies, synthesizing trait data, and developing simulation models (Wisnoski et al. 2019). This work showed how dormancy might affect community assembly, structure, and dynamics in varying ways, depending on species' capacities for dispersal, dormancy, and dispersal-dormancy covariation.

I also demonstrated with empirical data that dispersal and dormancy interact to affect aquatic bacterial community assembly. Freshwater ecosystems receive substantial inputs of organic matter, nutrients, and organisms from the surrounding terrestrial ecosystem (Polis et al. 1997, 2004; Gounand, Little, et al. 2018). However, the implications of these terrestrial inputs for the assembly of aquatic bacterial communities is not yet fully understood. Because fluxes of microorganisms and resources across the terrestrial-aquatic interface may be coupled (Ruiz-González, Niño-García, Lapierre, et al. 2015), the combined terrestrial and aquatic ecosystems may be considered a meta-ecosystem (Loreau, Mouquet, and Holt 2003; Gounand, Harvey, et al. 2018). Meta-ecosystem theory suggests, however, that the dispersal of organisms across sharp environmental gradients, such as the terrestrial-aquatic interface, may have limited effects on recipient communities because dispersers are unlikely to survive in both habitats (Massol et al. 2017; Gounand, Harvey, et al. 2018), unless resource subsidies are high enough to homogenize the landscape (Gravel et al. 2010). Therefore, although dispersal rates from neighboring terrestrial ecosystems are high (Bergström and Jansson 2000) and have been hypothesized to strongly affect aquatic bacterial community structure

(Crump et al. 2012), we showed in Chapter 4 that most of these cross-boundary dispersers are likely dormant, with only a subset colonizing and becoming metabolically active in the aquatic ecosystem (Wisnoski et al. 2020). This chapter demonstrates that dormancy may be key for understanding the effects of terrestrial contributions to aquatic bacterial communities and provides an example of how dormancy may affect metacommunities and meta-ecosystems more broadly.

Future directions

Ecological communities are structured by a multitude of processes interacting across space and time. While my dissertation has examined a few of these processes (e.g., dispersal, dormancy, environmental filtering), several important features of microbial metacommunities deserve further attention.

Phenotypic heterogeneity and plasticity — Intraspecific trait variation has important consequences for community structure and dynamics (Bolnick et al. 2011; Violle et al. 2012; Des Roches et al. 2017). For example, intraspecific variation can affect communities through nonlinear relationships between trait values and species interactions (i.e., Jensen's inequality), trait-dependent interaction networks, or dampened population dynamics arising from portfolio effects (Bolnick et al. 2011), which can modify coexistence outcomes (Hart et al. 2016). Microorganisms exhibit high phenotypic heterogeneity among individuals (West et al. 2007; Ackermann 2015; Hellweger et al. 2016), spanning traits related to division of labor in biofilms (Gestel et al. 2015), dispersal strategies and propensities (McDougald et al. 2011), levels of metabolic activity (Lennon and Jones 2011; Şimşek and Kim 2018), susceptibility to phages or antibiotic compounds (Pearl et al. 2008; Sánchez-Romero and Casadesús 2014; Fisher et al. 2017), and cellular age (Moger-Reischer and Lennon 2019). The effects of phenotypic heterogeneity can have implications that affect multiple spatial scales (Banitz 2019). For example, variation in individual dispersal kernels or resource requirements can alter metacommunity dynamics by regulating the balance between local and regional processes. This intraspecific trait variation may be stochastic, genetic, or environmentally induced, and plastic phenotypes can potentially vary over individual lifespans. Investigating the

roles of phenotypic heterogeneity and plasticity in metacommunities is likely to reveal new insights into our understanding of how complex communities are structured across space and time.

Evolutionary dynamics — Evolutionary processes can have profound consequences for ecological communities and the maintenance of diversity (Fussmann et al. 2007; Schoener 2011; Hendry 2017). Heritable intraspecific trait variation can allow different phenotypes to be favored over time, which can, for example, promote evolutionary rescue of at-risk populations (Gomulkiewicz and Holt 1995; Carlson et al. 2014; Bell 2017), modify consumer-resource dynamics (Yoshida et al. 2003; Kinnison et al. 2015), and alter spatial patterns of biodiversity (Thompson 2005; Brockhurst et al. 2006; Urban and De Meester 2009). Examinations of eco-evolutionary feedbacks in a metacommunity context suggest that the relationship between dispersal and local adaptation may be critical for shaping patterns of diversity across larger scales of space and time (Loeuille and Leibold 2008; De Meester et al. 2016; Vanoverbeke et al. 2016; Leibold et al. 2019). While evolutionary dynamics can influence the maintenance of diversity across scales of space, time, and biological organization, many important questions remain. For instance, little is known about the biotic or abiotic conditions under which ecological coexistence mechanisms (e.g., storage effects, nonlinear functional responses, fitness equivalence) evolve in local communities or across larger spatial scales (Pfennig and Pfennig 2009; Abrams et al. 2013; Germain et al. 2018). Furthermore, although trait covariance can constrain evolutionary (and ecological) outcomes (Nuismer and Doebeli 2004), it remains far from clear how trait covariation (e.g., between dispersal and dormancy) affects eco-evolutionary dynamics in diverse communities across spatial scales. Thus, tighter integration between ecological and evolutionary processes may uncover the complex feedbacks responsible for generating the patterns of diversity found in nature that have yet to be fully explained.

Stochasticity — The importance of stochasticity in populations and communities has been recognized for decades (Andrewartha and Birch 1954; Schaffer et al. 1986; Lande 1993; Halley 1996). However, the potential insights than can be gleaned from the structure of demographic or environmental stochasticity (e.g., noise color, spatial and temporal patterns) have not been fully appreciated in community and metacommunity ecology (Boettiger 2018; Shoemaker et al. 2020). For exam-

ple, noise color (i.e., temporally autocorrelated residuals) can generate prolonged deviations from seasonal norms (e.g., atypically long droughts during positively autocorrelated red noise) or erratic fluctuations akin to "weather whiplash" (e.g., extreme conditions above and below historical trends associated with negatively autocorrelated blue noise). Noise color can have effects on population dynamics (Kaitala et al. 1997; Vasseur and Yodzis 2004), community structure and coexistence (Ruokolainen and Fowler 2008; Ruokolainen et al. 2009), and diversity at larger spatial scales (Caswell and Cohen 1995; Ruokolainen 2013; Marshall and Burgess 2015). The effects of noise color on species coexistence across scales also depend on the relationship between spatial and temporal variation in the environment, as well as on species' traits in the community (Snyder 2008). These groundbreaking studies demonstrate that there is still much to be learned about how spatially or temporally structured stochasticity affects ecological outcomes across scales of organization.

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APPENDIX A

SUPPLEMENTAL INFORMATION FOR *MICROBIAL COMMUNITY ASSEMBLY IN A MULTI-LAYER DENDRITIC COMMUNITY*

A.1 Diversity patterns

We detected habitat differences in observed α-diversity in the stream network. As described in the main text, planktonic communities had higher diversity and more habitat-specific taxa (Fig. A.1) than sediment-associated communities.

A.2 Scale-dependence in βNTI

We detected habitat differences in the spatial scaling of phylogenetic β-diversity in the stream network. In the main text, we described scale-dependence of the relative importance of inferred community assembly mechanisms. Here, I show the scale-dependent patterns of βNTI, which was used to infer convergent (βNTI < -2) versus divergent (βNTI > 2) species sorting (Fig. A.2). In particular, sediment communities showed variable patterns of convergent or divergent species sorting for comparisons across all dendritic distances. But, on average, βNTI was < -2, indicating overall convergence, as reported in the main text. In contrast, planktonic communities showed a scale-dependent transition from convergent sorting at local scales (βNTI < -2) to divergent species sorting at regional scales (βNTI > 2). When comparisons were made betweed planktonic and sediment-associated communities, divergent sorting was evident across all scales (βNTI > 2), but the degree of divergence increased with greater spatial distance between the communities in the network.

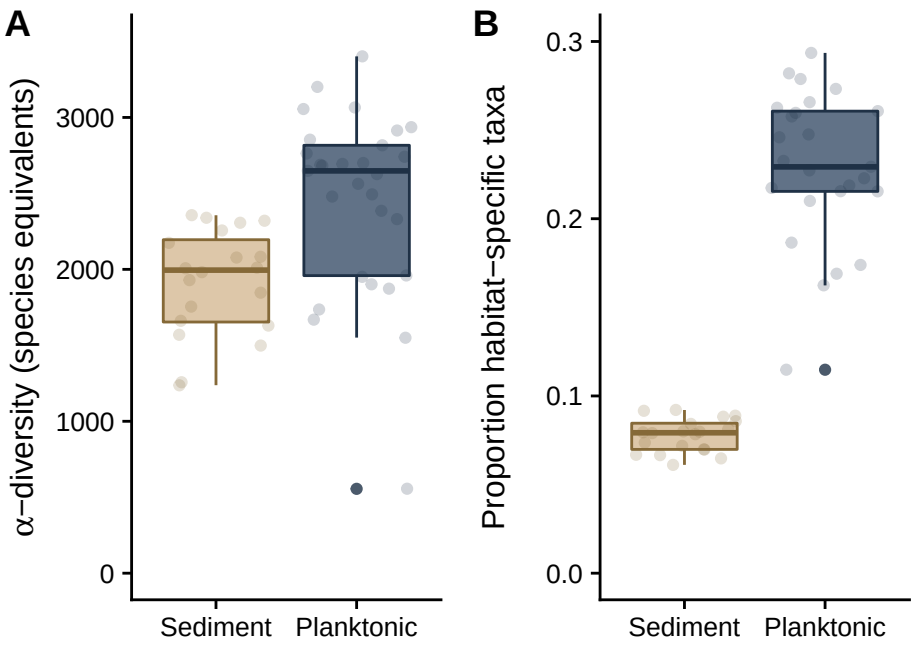

Figure A.1: Planktonic communities had (A) higher α-diversity and (B) a larger proportion of habitat-specific taxa than sediment-associated communities.

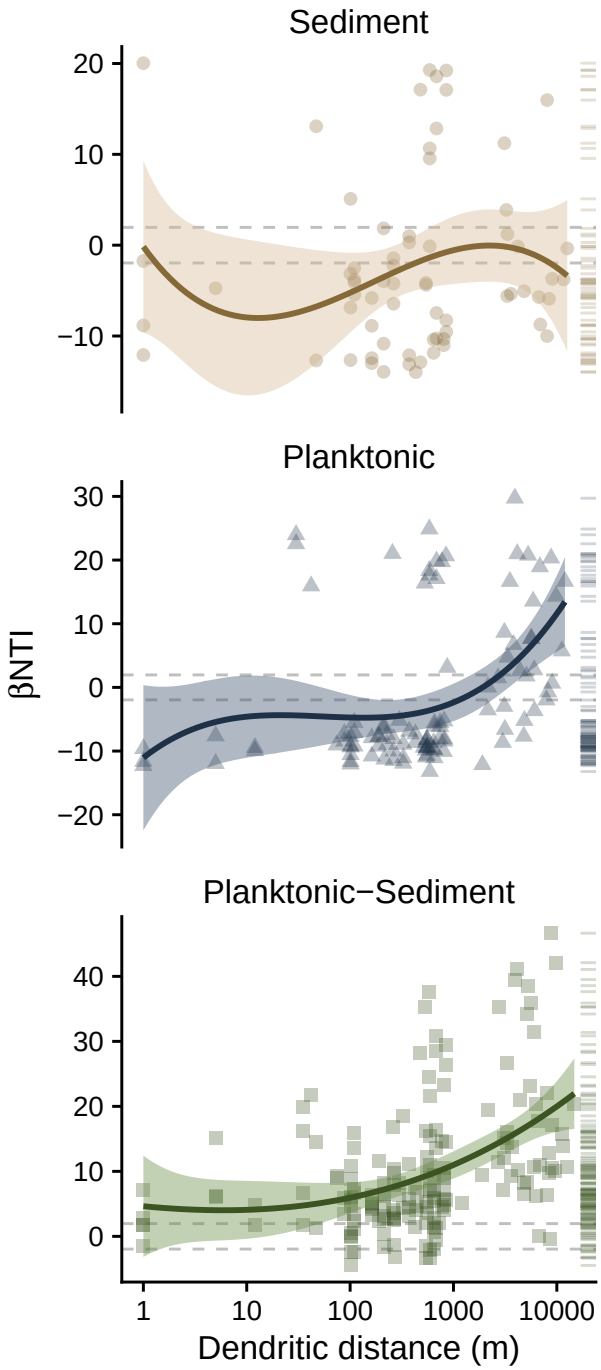

Figure A.2: Habitat differences in the spatial scaling of βNTI. Sediment communities showed variable patterns of convergent or divergent species sorting across dendritic distances. Planktonic communities showed a scale-dependent transition from convergent sorting at local scales (βNTI < -2) to divergent species sorting at regional scales (βNTI > 2). Divergent sorting between planktonic and sediment habitats was evident across all scales (βNTI > 2), but the degree of divergence increased with greater spatial distance between the communities in the network.

APPENDIX B

SUPPLEMENTAL INFORMATION FOR *STABILIZING BIOTIC INTERACTIONS AND SEED BANK DYNAMICS MAINTAIN FRESHWATER BACTERIAL DIVERSITY*

Included in this supplement are additional figures from the temporal study on bacterioplankton community dynamcis in University Lake.

B.1 Environmental variability

We tracked environmental variables in University Lake (Fig. B.1). In particular, we saw strong seasonality of temperature. Other variables were less seasonal, but still exhibited wide variability.

For the 82 persistent taxa identified in University Lake, we tested whether they might undergo temporal niche partitioning along environmental fluctuations. For the time of the year when each OTU experienced its maximum growth rate (an index of seasonal preference), we compared how environmental differences varied among taxa. To visualize this, we performed a principal component analysis (PCA) on the following environmental variables (standardized to mean = 0 and standard deviation = 1): temperature, specific conductivity, Secchi depth, pH, TP, TN, and DOC. We then plotted the time point where maximum growth was observed for the 82 taxa along the environmental space outlined by the first two PC axes (Fig. B.2). Points were color-coded by month following the scheme in the main text, and loading vectors describing environmental conditions along axes PC1 and PC2 were plotted.

From this analysis, we see that different OTUs were favored at different periods of time corresponding to variation in environmental conditions. For example, some taxa grew best when nitrogen and phosphorus were high and temperature was low, others when pH was highest, and others when dissolved oxygen was high. This provides further evidence that environmental variation regulated bacterioplankton dynamics in the lake.

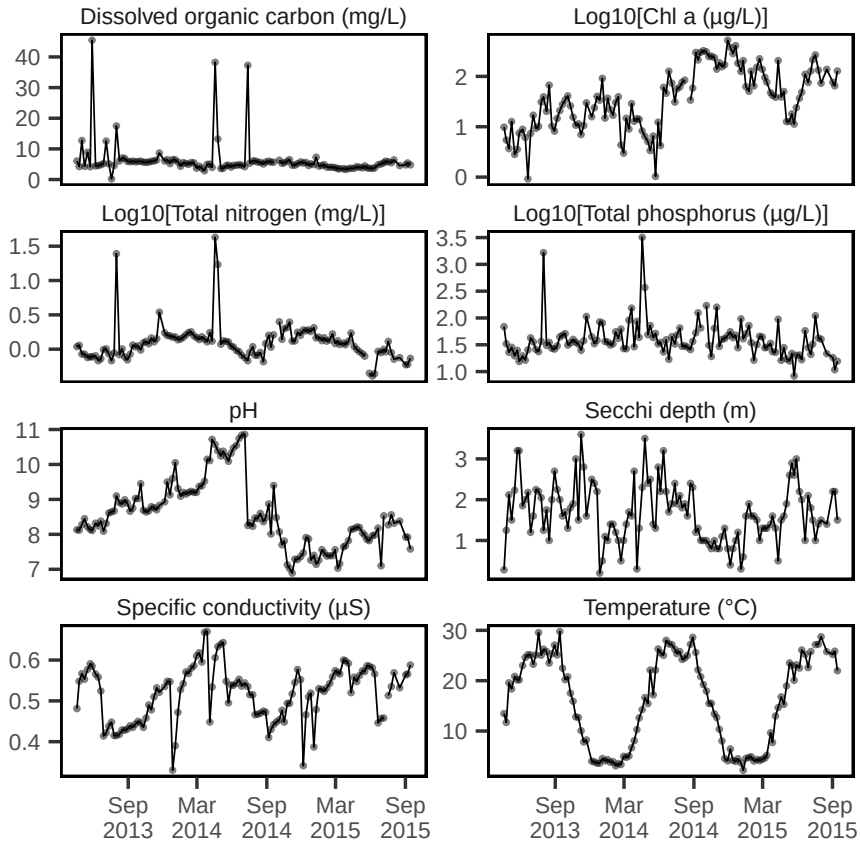

Figure B.1: Temporal variability in environmental conditions in University Lake, Indiana. Large pulses of DOC, TP, and TN could reflect terrestrial inputs from the surrounding watershed.

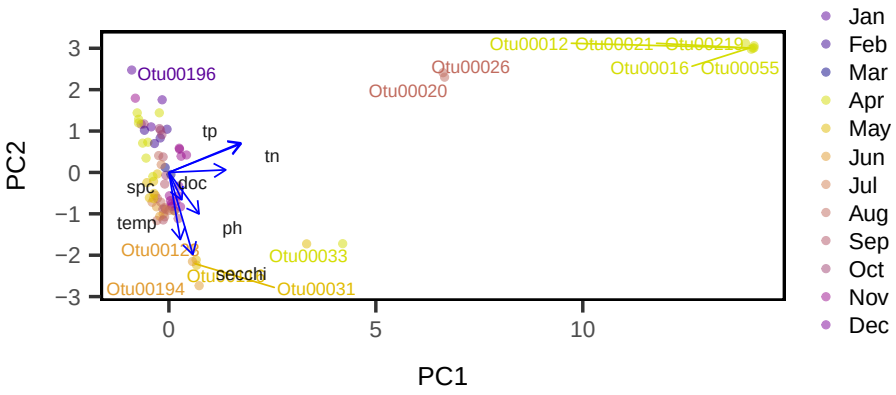

Figure B.2: Temporal partitioning of max growth rates also corresponds to environmental conditions.

B.2 Negative frequency dependent growth

We analyzed negative frequency dependence in the data. NFD occurs when populations have higher growth when rare than when common (Fig. B.3). When NFD is stronger for rare taxa than for common taxa (Fig. B.4), rare taxa may be stabilized by the ability to recover from rarity as population size declines (Yenni et al. 2012). This would indicate the presence of stabilizing coexistence mechanisms maintaining diversity in the community (Yenni et al. 2017).

First, we detected negative frequency dependence in the 82 persistent taxa (Fig. B.5). That is, populations had higher growth rates at lower relative abundances and lower growth rates when common.

Thus, we have shown that NFD occurs among the persistent taxa in the community. The analysis in the main text expands on this phenomenon by asking whether rarer taxa have stronger NFD than common taxa. In our anlysis, we found support for this hypothesized asymmetry in NFD (Fig. B.7). Asymmetric NFD was detected across both active and total portions of the community (Fig. B.8). Interestingly, the slopes of the relationships were nearly identical in both portions of the community, but the active portion had wider variation in the extremes of the data range. In particular, NFD was stronger in rarer taxa and weaker in common taxa in the active community when compared with the total community. Intermediate frequencies were highly similar.

This negative covariance between equilibrium frequency and strength of NFD is expected by chance, however, and so we compared our observations to null distributions to determine whether the strength of the negative relationship was expected by chance alone. Indeed, we found that rare taxa experienced stronger NFD than common taxa only in the active portion of the community (Fig. 2.3), which may be explained by the fact that the persistent OTUs were rarer and showed stronger NFD in the active portion of the community than the total community (Fig. B.8).

We also investigated the sensitivity of NFD asymmetry to the number of taxa included in the analysis. By subsampling the data, including a range of OTUs in the analysis, we performed the asymmetric NFD analysis described in the main text (Yenni et al. 2017). We calculated standardized

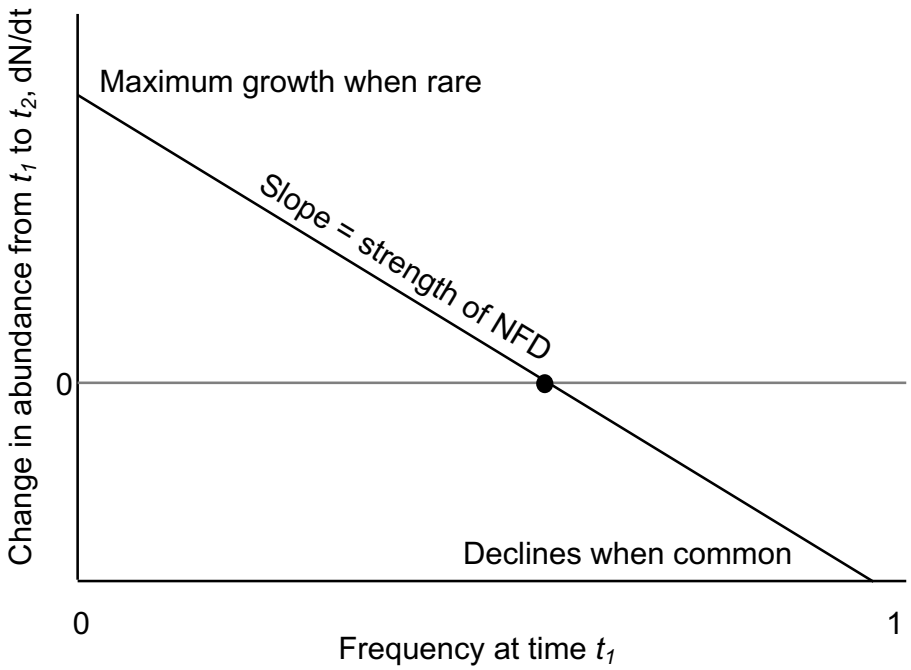

Figure B.3: Negative frequency dependence is strongest in rarer than common taxa. Here, NFD values are calculated on the active population.

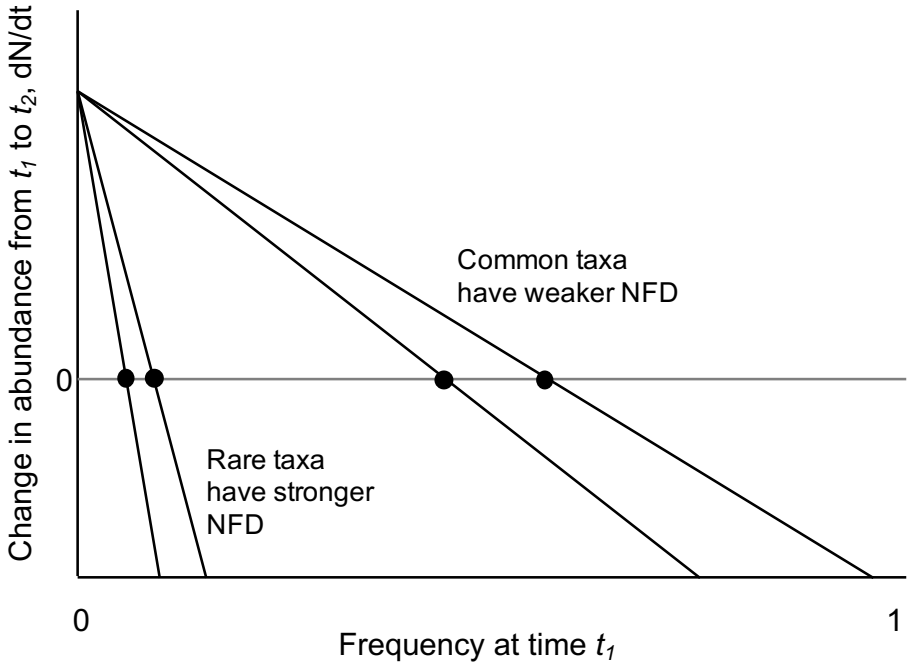

Figure B.4: Negative frequency dependence is strongest in rarer than common taxa. Here, NFD values are calculated on the active population.

effect sizes [SES = (observed covariance - mean covariance of null distribution) / standard deviation (null distribution)] to measure significant differences. If SES < -2, rare species had stronger NFD than common species. We found evidence for asymmetric NFD across a range of included taxa (Fig. B.9).

B.3 Phylogenetic inference

We analyzed whether taxonomic responses to environmental variability were more similar among closely related taxa. First, we created a phylogeny using approximately maximum likelihood methods in FastTree (Price et al. 2010). Then, we subset the tree to the 82 persistent taxa used in the analysis. We generated a phylogenetic tree using the ggtree R package (Yu et al. 2017). For each OTU on the tree, we visualized the average growth rate detected in each month as a heatmap. Our analysis shows that similar taxa do not show strongly similar annual growth dynamics, but instead there is wide variation in growth patterns within clades and across the tree (Fig. B.10).

B.4 Persistent taxa

Throughout this analysis, we have focused on 82 OTUs that persisted across the time series. In particular, these taxa were detected in 80% of DNA samples, suggesting they are core members of the bacterioplankton community in University Lake. We provide more information here on their taxonomy, maximum growth rates, and timing of maximum growth (Table B.1).

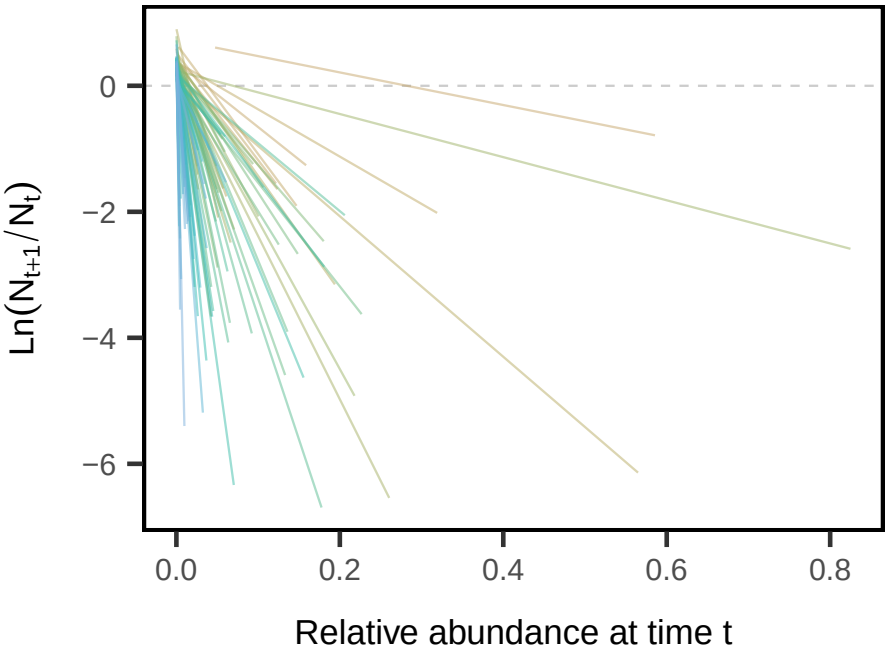

Figure B.5: Negative frequency dependence was present in both the active (shown here) and total communities. Here, we depict the relationship between the relative abundance of each OTU at time t and its rate of change in population size from time t (N_t) to $t + 1$ (N_{t+1}).

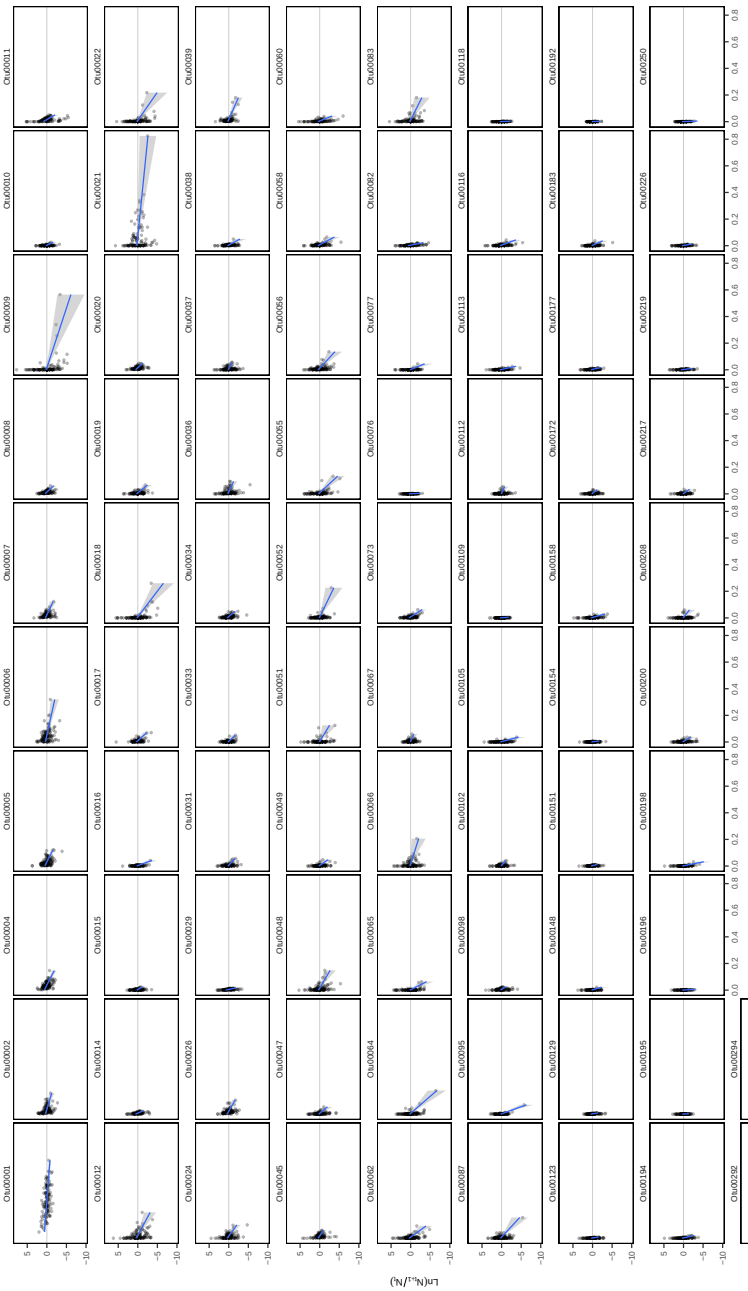

Figure B.6: NFD relationships for each persistent OTU in the active portion of the community. This figure presents the raw data behind the slopes depicted in Fig. B.5.

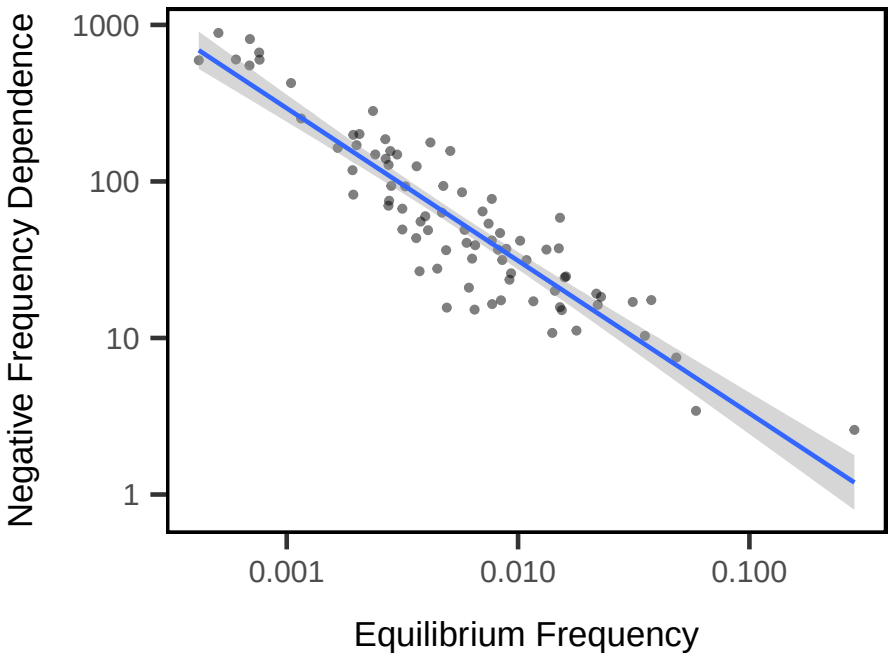

Figure B.7: Negative frequency dependence is strongest in rarer than common taxa. Here, NFD values are calculated on the active population.

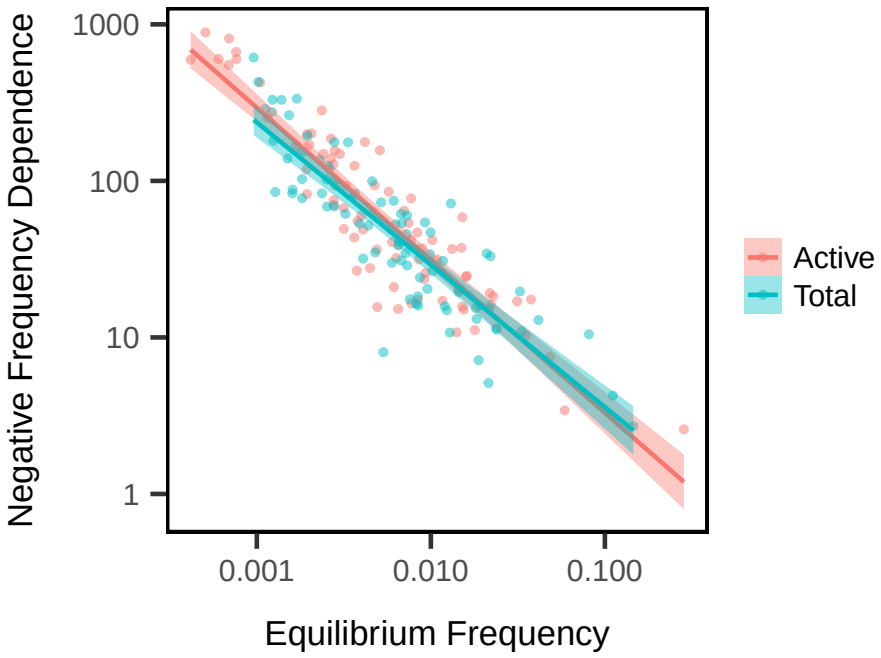

Figure B.8: The relationship between negative frequency dependence and equilibrium frequency is the same in active and total communities. However, the maximum NFD observed in the active portion of the community (for rare taxa) is much higher than the max observed in the total community.

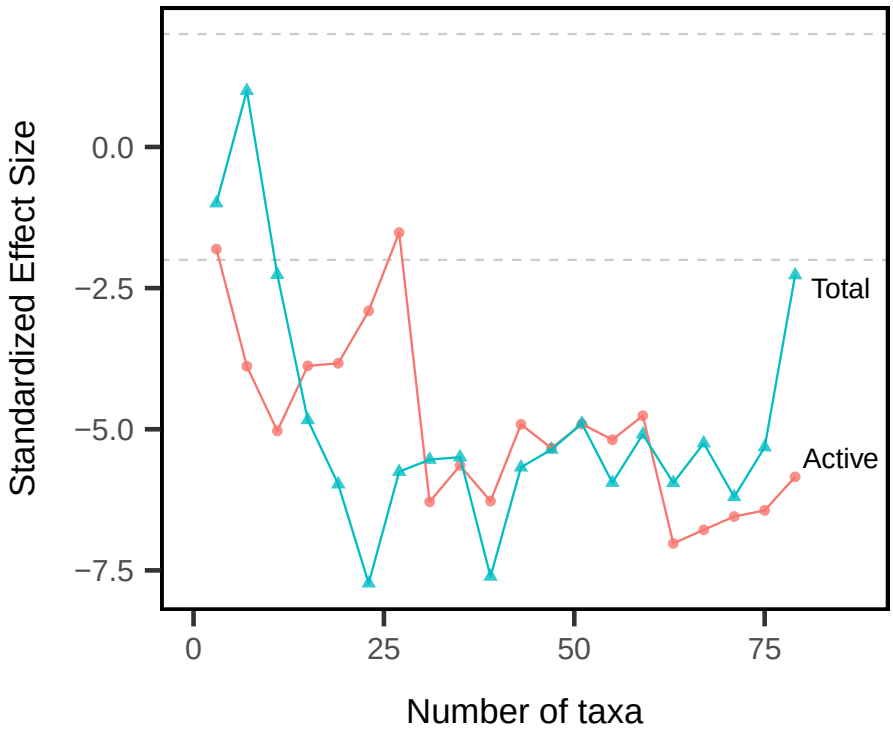

Figure B.9: Sensitivity of the strength of NFD in the active and total portions of the committee as a function of the number of OTUs included in the analysis.

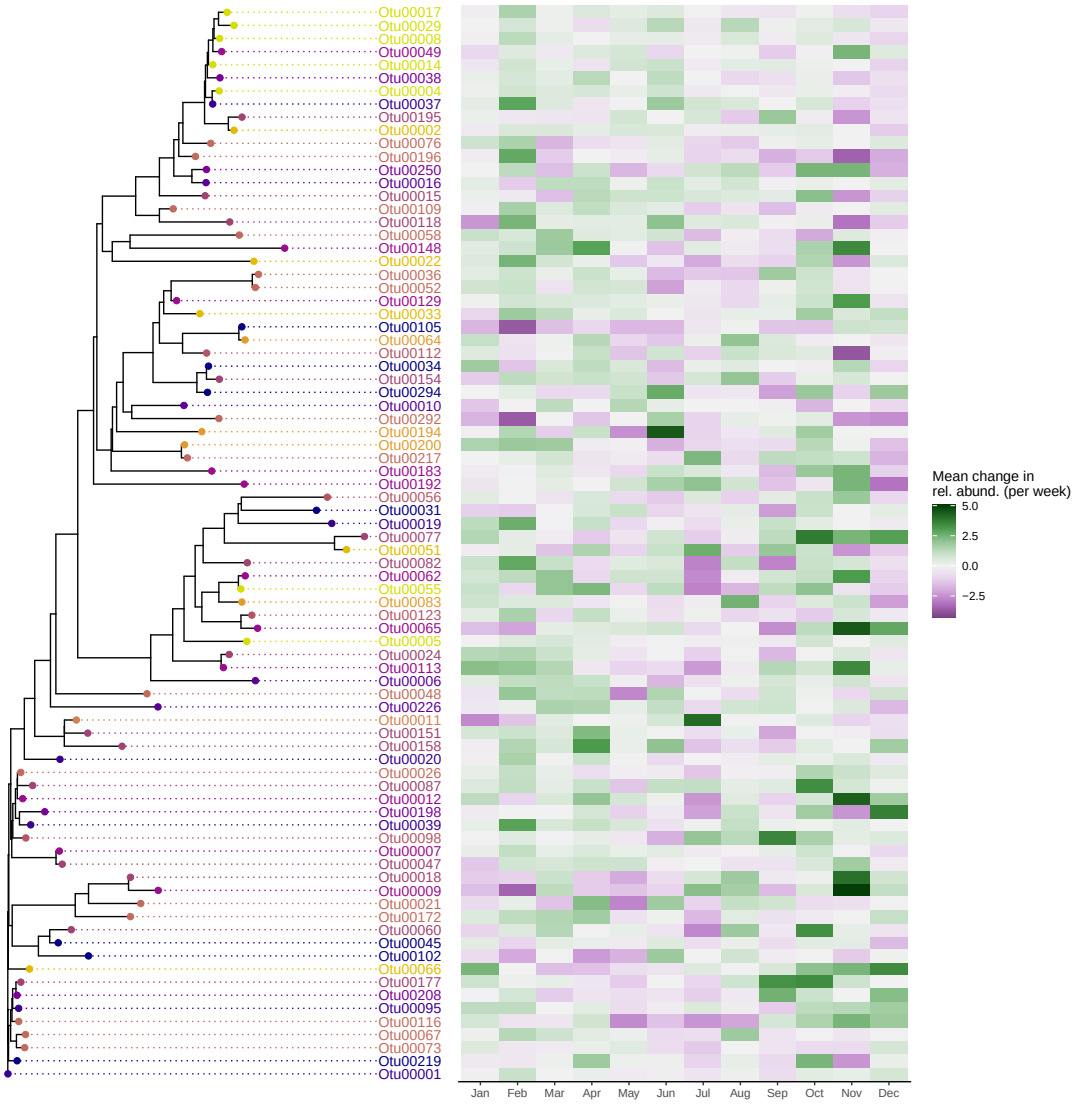

Figure B.10: Seasonal growth dynamics appear unrelated to phylogenetic relatedness among 82 persistent bacterial taxa in University Lake.

Table B.1: Persistent taxa from University Lake. These taxa were detected in at least 80% of the DNA samples from the time series.

OTU	Phylum	Class	Order	Family	Genus
Otu00034	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingorhabdus
Otu00045	Proteobacteria	Betaproteobacteria	Burkholderiales	Oxalobacteraceae	Oxalobacteraceae sp.
Otu00196	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00019	Bacteroidetes	Cytophagia	Cytophagales	Cytophagaceae	Cytophagaceae sp.
Otu00039	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Comamonas
Otu00102	Proteobacteria	Betaproteobacteria	Methylophilales	Methylophilaceae	Methylophilus
Otu00105	Proteobacteria	Alphaproteobacteria	Caulobacterales	Caulobacteraceae	Brevundimonas
Otu00065	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Sphingobacteriaceae	Pedobacter
Otu00292	Proteobacteria	Alphaproteobacteria	Alphaproteobacteria sp.	Alphaproteobacteria sp.	Alphaproteobacteria sp.
Otu00006	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Saprospiraceae	Saprospiraceae sp.
Otu00012	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Comamonadaceae sp.
Otu00014	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00016	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Microbacteriaceae sp.
Otu00017	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00021	Proteobacteria	Gammaproteobacteria	Methylococcales	Methylococcaceae	Methylococcaceae sp.
Otu00033	Proteobacteria	Alphaproteobacteria	Rhizobiales	Rhizobiales sp.	Rhizobiales sp.
Otu00048	Verrucomicrobia	Verrucomicrobiae	Verrucomicrobiales	Verrucomicrobiaceae	Prosthecobacter
Otu00049	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00055	Bacteroidetes	Flavobacteriia	Flavobacteriales	Cryomorphaceae	Cryomorphaceae sp.
Otu00058	Armatimonadetes	Armatimonadia	Armatimonadales	Armatimonadaceae	Armatimonas
Otu00148	Bacteria sp.	Bacteria sp.	Bacteria sp.	Bacteria sp.	Bacteria sp.
Otu00172	Proteobacteria	Gammaproteobacteria	Gammaproteobacteria sp.	Gammaproteobacteria sp.	Gammaproteobacteria sp.
Otu00219	Proteobacteria	Betaproteobacteria	Burkholderiales	Burkholderiales sp.	Burkholderiales sp.
Otu00002	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00008	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00022	Verrucomicrobia	Opitutae	Opitutae sp.	Opitutae sp.	Opitutae sp.
Otu00031	Bacteroidetes	Cytophagia	Cytophagales	Cyclobacteriaceae	Algoriphagus
Otu00051	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Flavobacterium
Otu00062	Bacteroidetes	Flavobacteriia	Flavobacteriales	Cryomorphaceae	Cryomorphaceae sp.
Otu00064	Proteobacteria	Alphaproteobacteria	Caulobacterales	Caulobacteraceae	Brevundimonas
Otu00113	Bacteroidetes	Bacteroidetes sp.	Bacteroidetes sp.	Bacteroidetes sp.	Bacteroidetes sp.
Otu00116	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Comamonadaceae sp.
Otu00151	Proteobacteria	Betaproteobacteria	Betaproteobacteria sp.	Betaproteobacteria sp.	Betaproteobacteria sp.
Otu00183	Bacteria sp.	Bacteria sp.	Bacteria sp.	Bacteria sp.	Bacteria sp.

Table B.1 continued from previous page

OTU	Phylum	Class	Order	Family	Genus
Otu00200	Bacteria sp.	Bacteria sp.	Bacteria sp.	Bacteria sp.	Bacteria sp.
Otu00083	Bacteroidetes	Flavobacteriia	Flavobacteriales	Cryomorphaceae	Fluviicola
Otu00087	Proteobacteria	Betaproteobacteria	Burkholderiales	Burkholderiales incertae sedis	Aquabacterium
Otu00098	Proteobacteria	Betaproteobacteria	Burkholderiales	Burkholderiales sp.	Burkholderiales sp.
Otu00123	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Sphingobacteriaceae	Pedobacter
Otu00194	Proteobacteria	Deltaproteobacteria	Bdellovibrionales	Bacteriovoracaceae	Peredibacter
Otu00294	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Novosphingobium
Otu00004	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00009	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Pseudomonas
Otu00011	Proteobacteria	Betaproteobacteria	Betaproteobacteria sp.	Betaproteobacteria sp.	Betaproteobacteria sp.
Otu00192	Bacteria sp.	Bacteria sp.	Bacteria sp.	Bacteria sp.	Bacteria sp.
Otu00195	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00020	Proteobacteria	Betaproteobacteria	Burkholderiales	Alcaligenaceae	Alcaligenaceae sp.
Otu00026	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Comamonadaceae sp.
Otu00029	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00036	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraceae sp.
Otu00037	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00052	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraceae sp.
Otu00076	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.
Otu00112	Proteobacteria	Alphaproteobacteria	Caulobacterales	Caulobacteraceae	Caulobacter
Otu00226	Verrucomicrobia	Opitutae	Opitutales	Opitutaceae	Opitutus
Otu00250	Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Microbacteriaceae sp.
Otu00010	Proteobacteria	Proteobacteria sp.	Proteobacteria sp.	Proteobacteria sp.	Proteobacteria sp.
Otu00024	Bacteroidetes	Bacteroidetes sp.	Bacteroidetes sp.	Bacteroidetes sp.	Bacteroidetes sp.
Otu00056	Bacteroidetes	Cytophagia	Cytophagales	Cytophagaceae	Emticicia
Otu00067	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Comamonadaceae sp.
Otu00177	Proteobacteria	Proteobacteria sp.	Proteobacteria sp.	Proteobacteria sp.	Proteobacteria sp.
Otu00005	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Chitinophagaceae	Sediminibacterium
Otu00015	Actinobacteria	Actinobacteria	Actinobacteria sp.	Actinobacteria sp.	Actinobacteria sp.
Otu00018	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Pseudomonas
Otu00060	Proteobacteria	Betaproteobacteria	Burkholderiales	Burkholderiaceae	Polynucleobacter
Otu00066	Proteobacteria	Betaproteobacteria	Burkholderiales	Burkholderiales sp.	Burkholderiales sp.
Otu00082	Bacteroidetes	Bacteroidetes sp.	Bacteroidetes sp.	Bacteroidetes sp.	Bacteroidetes sp.
Otu00154	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingorhabdus
Otu00158	Proteobacteria	Gammaproteobacteria	Gammaproteobacteria sp.	Gammaproteobacteria sp.	Gammaproteobacteria sp.
Otu00001	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Comamonadaceae sp.
Otu00007	Proteobacteria	Betaproteobacteria	Burkholderiales	Burkholderiaceae	Polynucleobacter
Otu00038	Actinobacteria	Actinobacteria	Actinomycetales	Actinomycetales sp.	Actinomycetales sp.

Table B.1 continued from previous page

OTU	Phylum	Class	Order	Family	Genus
Otu00047	Proteobacteria	Betaproteobacteria	Burkholderiales	Burkholderiaceae	Polynucleobacter
Otu00073	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Polaromonas
Otu00077	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	Flavobacterium
Otu00109	Actinobacteria	Actinobacteria	Acidimicrobiales	Acidimicrobiales sp.	Acidimicrobiales sp.
Otu00118	Actinobacteria	Actinobacteria	Actinobacteria sp.	Actinobacteria sp.	Actinobacteria sp.
Otu00129	Proteobacteria	Alphaproteobacteria	Rhizobiales	Beijerinckiaceae	Beijerinckia
Otu00198	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Hydrogenophaga
Otu00208	Proteobacteria	Betaproteobacteria	Burkholderiales	Burkholderiales sp.	Burkholderiales sp.
Otu00217	Proteobacteria	Proteobacteria sp.	Proteobacteria sp.	Proteobacteria sp.	Proteobacteria sp.
Otu00095	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Comamonadaceae sp.

Table B.2:

OTU	Class	Max growth rate (per week)	Date of max growth
Otu00034	Alphaproteobacteria	2.398	2014-01-17
Otu00045	Betaproteobacteria	5.969	2014-01-03
Otu00196	Actinobacteria	4.111	2015-01-09
Otu00019	Cytophagia	5.142	2014-02-14
Otu00039	Betaproteobacteria	5.017	2014-02-14
Otu00102	Betaproteobacteria	4.71	2015-02-28
Otu00105	Alphaproteobacteria	6.066	2014-02-28
Otu00065	Sphingobacteriia	5.994	2014-03-21
Otu00292	Alphaproteobacteria	4.796	2014-03-07
Otu00006	Sphingobacteriia	2.55	2013-04-25
Otu00012	Betaproteobacteria	6.149	2014-04-18
Otu00014	Actinobacteria	3.434	2015-04-26
Otu00016	Actinobacteria	5.485	2014-04-18
Otu00017	Actinobacteria	7.14	2015-04-04
Otu00021	Gammaproteobacteria	7.314	2014-04-18
Otu00033	Alphaproteobacteria	3.714	2014-04-25
Otu00048	Verrucomicrobiae	5.198	2015-04-11
Otu00049	Actinobacteria	4.263	2014-04-04
Otu00055	Flavobacteriia	5.565	2014-04-18
Otu00058	Armatimonadia	5.707	2015-04-11
Otu00148	Bacteria sp.	5.352	2013-04-25
Otu00172	Gammaproteobacteria	4.71	2015-04-11
Otu00219	Betaproteobacteria	5.252	2014-04-18
Otu00002	Actinobacteria	2.233	2015-05-03
Otu00008	Actinobacteria	2.546	2013-05-09
Otu00022	Opitutae	5.602	2015-05-03
Otu00031	Cytophagia	4.615	2014-05-09
Otu00051	Flavobacteriia	6.431	2013-05-09
Otu00062	Flavobacteriia	5.485	2015-05-23
Otu00064	Alphaproteobacteria	4.875	2013-05-29
Otu00113	Bacteroidetes sp.	5.565	2013-05-09
Otu00116	Betaproteobacteria	5.861	2014-05-09
Otu00151	Betaproteobacteria	5.081	2013-05-17
Otu00183	Bacteria sp.	4.263	2015-05-03
Otu00200	Bacteria sp.	4.796	2015-05-23
Otu00083	Flavobacteriia	7.022	2015-06-06
Otu00087	Betaproteobacteria	4.111	2014-06-05
Otu00098	Betaproteobacteria	5.673	2013-06-14
Otu00123	Sphingobacteriia	5.081	2014-06-20
Otu00194	Deltaproteobacteria	6.494	2014-06-13
Otu00294	Alphaproteobacteria	4.875	2013-06-21
Otu00004	Actinobacteria	2.45	2015-07-11
Otu00009	Gammaproteobacteria	9.33	2013-07-26
Otu00011	Betaproteobacteria	6.889	2015-07-18
Otu00192	Bacteria sp.	3.045	2013-07-26
Otu00195	Actinobacteria	4.394	2014-07-18
Otu00020	Betaproteobacteria	2.905	2013-08-01
Otu00026	Betaproteobacteria	4.394	2013-08-01
Otu00029	Actinobacteria	4.615	2013-08-23
Otu00036	Alphaproteobacteria	5.303	2013-08-16
Otu00037	Actinobacteria	5.352	2014-08-29
Otu00052	Alphaproteobacteria	4.511	2013-08-09
Otu00076	Actinobacteria	4.511	2014-08-08

Table B.2 continued from previous page

OTU	Class	Max growth rate (per week)	Date of max growth
Otu00112	Alphaproteobacteria	4.111	2014-08-23
Otu00226	Opitutae	4.71	2015-08-02
Otu00250	Actinobacteria	3.714	2013-08-23
Otu00010	Proteobacteria sp.	4.394	2014-09-26
Otu00024	Bacteroidetes sp.	5.081	2014-09-19
Otu00056	Cytophagia	5.398	2013-09-06
Otu00067	Betaproteobacteria	3.714	2015-09-02
Otu00177	Proteobacteria sp.	3.714	2013-09-20
Otu00005	Sphingobacteriia	3.706	2014-10-04
Otu00015	Actinobacteria	4.394	2014-10-17
Otu00018	Gammaproteobacteria	6.661	2014-10-11
Otu00060	Betaproteobacteria	7.022	2013-10-25
Otu00066	Betaproteobacteria	5.707	2013-10-25
Otu00082	Bacteroidetes sp.	5.602	2014-10-04
Otu00154	Alphaproteobacteria	4.949	2014-10-04
Otu00158	Gammaproteobacteria	6.399	2013-10-04
Otu00001	Betaproteobacteria	2.002	2013-11-15
Otu00007	Betaproteobacteria	3.204	2013-11-15
Otu00038	Actinobacteria	5.142	2014-11-29
Otu00047	Betaproteobacteria	4.71	2013-11-15
Otu00073	Betaproteobacteria	3.434	2013-11-22
Otu00077	Flavobacteriia	5.442	2013-11-15
Otu00109	Actinobacteria	4.71	2013-11-15
Otu00118	Actinobacteria	4.263	2013-11-22
Otu00129	Alphaproteobacteria	3.434	2013-11-15
Otu00198	Betaproteobacteria	6.447	2013-11-15
Otu00208	Betaproteobacteria	4.875	2013-11-22
Otu00217	Proteobacteria sp.	5.017	2013-11-22
Otu00095	Betaproteobacteria	3.434	2013-12-13

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APPENDIX C

SUPPLEMENTAL INFORMATION FOR *DORMANCY IN METACOMMUNITIES*

C.1 Simulation modeling

To examine the effects of dispersal and dormancy on metacommunity diversity, we created simulation models. In these simulations, we modeled population growth under different types of environmental variability, then analyzed diversity along gradients of dispersal using the parameters listed in table C.1. All simulations and analyses were performed in R (R Core Team 2018). All code is available on GitHub (`https://github.com/LennonLab/MCdorm`).

C.1.1 Population growth in the metacommunity

We adapted the metacommunity model of Shoemaker and Melbourne (Shoemaker and Melbourne 2016), which models metacommunity dynamics in discrete time, with global dispersal occurring following a round of local population growth. Prior to dispersal, within-patch population growth follows the Beverton-Holt model (Beverton and Holt 1957), where population growth is the product of the species intrinsic growth rate, the current population size, and a measure of intra- and interspecific competition:

$$N_{t+h,jx} = R_{jx} N_{t,jx} \frac{1}{1 + \sum_k \alpha_k N_{t,kx}},$$

where $N_{t+h,jx}$ is the population density of species j in patch x; R_{jx} is the intrinsic, density-independent growth rate of species j in patch x; $N_{t,jx}$ is the current population size; and

$$\frac{1}{1 + \sum_k \alpha_k N_{t,kx}}$$

is a measure of competition as the sum of competition coefficients, α_k, weighted by the abundances, $N_{t,kx}$, of all species k in the patch.

To regulate fitness differences in species across the heterogeneous landscape, we made R_{jx} a Gaussian function

$$R_{jx} = R_{\max} \exp\left(\frac{(E_{t,x} - E_{j,\text{opt}})^2}{2 \times \sigma^2_{j,\text{nb}}}\right),$$

where $E_{j,\text{opt}}$ is species j's environmental niche optimum, $\sigma^2_{j,\text{nb}}$ is its niche breadth, and $E_{t,x}$ is the current environmental condition in patch x at time t. Thus, increasing mismatch between species optima and the environment will lead to suboptimal growth during the time step.

Dispersal was global, meaning that all patches received an equal proportion of immigrants at each time step, and it occurred after local population growth. We introduced a simple dormancy transition between the active community and the seed bank that was modeled by a constant rate of entering and exiting dormancy, as might be expected under bet hedging. With dispersal and dormancy included, the full metacommunity model then becomes:

$$N_{t+1,jx} = N_{t+h,jx} + d_j \left(\sum_{z \neq x} \frac{N_{t+h,jz}}{p-1}\right) + \beta D_{t+h,jx} - \delta N_{t+h,jx}$$

$$D_{t+1,jx} = D_{t+h,jx}(1-m) + \gamma \times d_j \left(\sum_{z \neq x} \frac{D_{t+h,jz}}{p-1} - D_{t+h,jx}\right) - \beta D_{t+h,jx} + \delta N_{t+h,jx},$$

where $N_{t+1,jx}$ is the population size of the active population following population growth, and $D_{t+1,jx}$ is the population size of the dormant population of species j in patch x. The net effects of dispersal are determined for each species j as the sum across the total number of patches p, where immigrants arrive at a rate d_j from all patches $z \neq x$ where x is the focal patch. The transitions between active $N_{t+1,jx}$ and dormant $D_{t+1,jx}$ populations in the metacommunity depend on the parameters β, which is the activation rate of dormant propagules, δ, which is the rate of entering dormancy; and m, which is the mortality rate of dormant propagules. Dispersal-dormancy covariation is modeled at the extreme case of whether dormant propagules are able to disperse or not, with γ representing the covariation.

C.1.2 Environmental variability

To analyze how different types of environmental variability influence the importance of dormancy in the metacommunity, we examined three simple cases: static environments, static environments with local disturbances, and perfectly spatiotemporally asynchronous environments. Environmental conditions were modeled as a single environmental variable with a range of [0,1], which corresponds to species optima in the metacommunity.

Environmentally static landscapes can allow source-sink dynamics and mass effects to arise because the patches where species optima are well matched to the environment are able to serve as source patches (Fig. C.1). Spatial heterogeneity was created by setting each patch to a value in the range [0,1]. This environmental gradient from 0 to 1 was evenly partitioned among all p patches, ensuring each species was the best competitor in at least one patch.

When there are local disturbances, some form of recolonization is required for species to persist in the landscape, from either spatial dispersal or temporal dispersal (see main figure, Fig. 3.4). We implemented a local disturbance in the way of Shoemaker and Melbourne (2016), where disturbance followed a Bernoulli distribution for each patch independently according to an extinction rate, e. We imposed disturbance by removing all individuals present in the active patch but not dormant patch.

When the optimal environmental conditions fluctuate in both space and time, some degree of spatial or temporal dispersal is necessary for species to coexist (Fig. C.2). We enforced perfect asynchrony in spatiotemporal environmental fluctuations following Loreau et al. (Loreau, Mouquet, and Gonzalez 2003). Here, environmental fluctuations oscillate according to a sine wave where each patch is equally out of phase with all other patches, such that the environmental conditions in patch x, E_x, is determined by

$$E_x = \frac{1}{2}\left[\sin\left(E_{x,0} + \frac{2\pi t}{T}\right) + 1\right],$$

where $E_{x,0}$ is the starting environmental condition for each patch (partitioned equally, as above

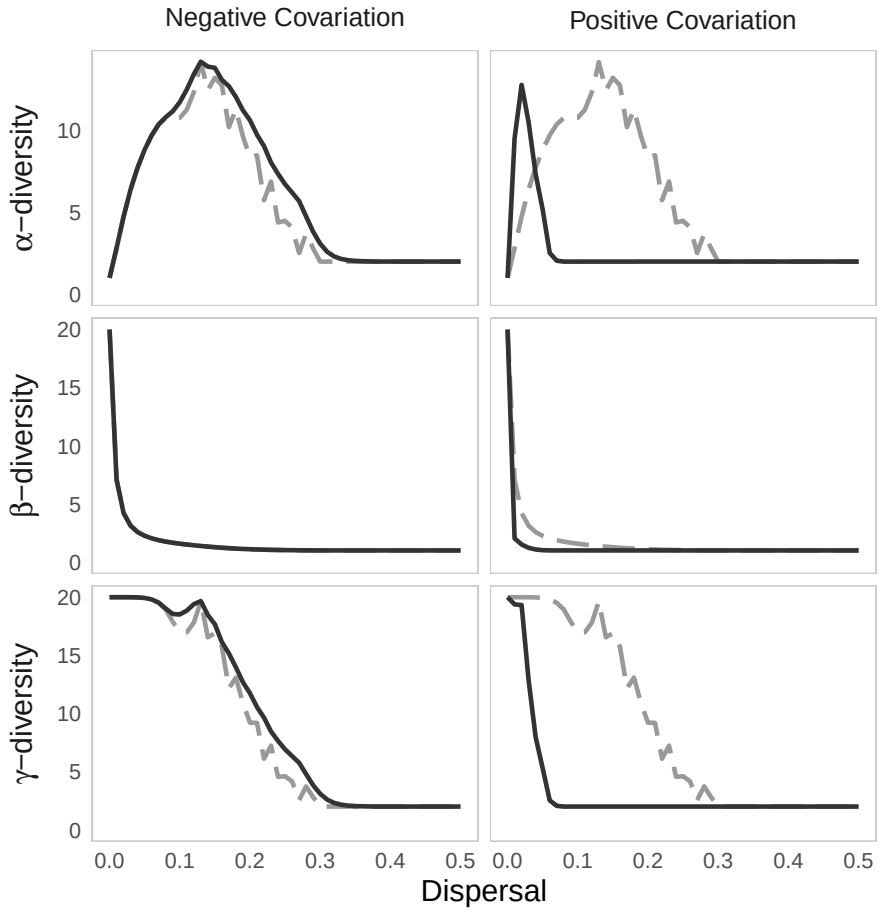

Figure C.1: Dispersal-diversity relationships with (dark solid line) and without (dashed light line) dormancy in a spatially heterogeneous but temporally static environment without disturbances. With negative dispersal-dormancy covariation, dormant propagules are simply lost to the seed bank because they do not disperse. As a result, dormancy does not improve persistence under temporally static conditions. With positive dispersal-dormancy covariation, dormancy maintains a-diversity at low dispersal rates but also rapidly increases the onset of homogenization.

Table C.1: Model parameters for simulations

Parameter	Symbol	Value(s)
No. sites	p	20
No. species	k	20
Disturbance frequency	e	$[0, .001]$
Environmental period	T	$1,000$
Niche breadth	σ^2	.5
Intrinsic growth rate	R_{max}	1.2
Strength of competition	α_k	4×10^{-4}
Dormant decay rate	m	1×10^{-6}
Dormancy rate	δ	.7
Reactivation rate	β	.1
Dispersal-dormancy covariation	γ	$[0, 1]$

in the static landscape), t is the current time step, T is the period of oscillations, such that longer periods converge on the static model and shorter periods fluctuate rapidly enough to converge on a single average patch of intermediate quality.

C.1.3 Diversity Partitioning Analysis

Our partitioning of diversity across spatial scales into local (α), regional (γ), and among-site (β) diversity follows the multiplicative approach of Whittaker (Whittaker 1972), as modified by Jost (Jost 2007) and implemented in the 'vegetarian' R package (Charney and Record 2012). Therefore, the relationship between α, β, and γ is

$$\beta = \frac{\gamma}{\overline{\alpha}},$$

where γ is diversity measured on the scale of the entire metacommunity and $\overline{\alpha}$ is the average diversity at the local scale. In this analysis, diversity is measured in units of species equivalents or Hill numbers at the order ($q = 1$), which corresponds to the number of equally abundant species needed to reach the observed value of diversity measured by the Shannon index.

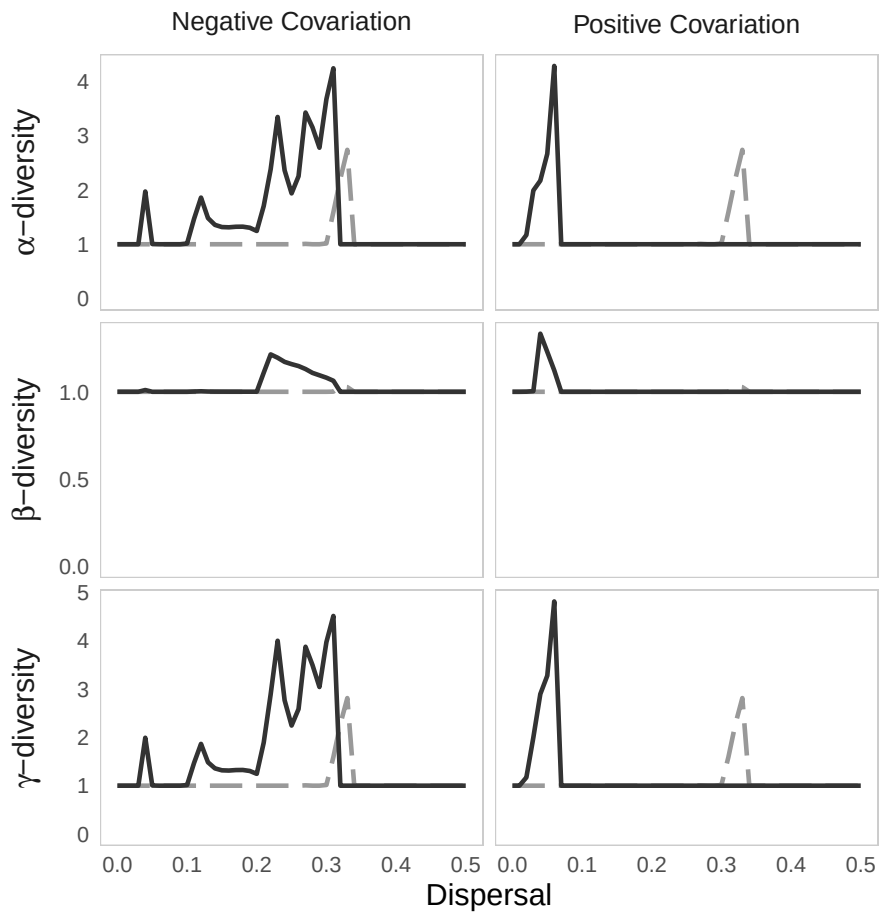

Figure C.2: Dispersal-diversity relationships with (dark solid line) and without (dashed light line) dormancy in an environment that exhibits asynchrony in space and time. With negative dispersal-dormancy covariation (i.e., a trade-off), dormancy increases α- and γ-diversity and maintains β-diversity under dispersal limitation (i.e., at low dispersal rates), but it cannot protect against homogenization (diversity plummets at the same rate with increasing dispersal, regardless of dormancy). With positive dispersal-dormancy covariation, dormancy lowers the dispersal rate that maximizes α-, β-, and γ-diversity; increases maximum α- and γ-diversity; and also increase the homogenizing effects of dispersal. The metacommunity with dormancy is homogenized (i.e., one species dominates) at dispersal rates that were limiting in the absence of dormancy.

C.2 Bromeliad community trait data analysis

C.2.1 Data set

To demonstrate a potential approach to assessing dispersal-dormancy covariation in a metacommunity context, we analyzed a large trait dataset of taxa commonly operating as a metacommunity. Twelve functional traits were measured for 852 aquatic invertebrate taxa that live in the pools of water that accumulate in bromeliad plants (Céréghino et al. 2018). The data are available to download from the Knowledge Network for Biocomplexity at `https://doi.org/10.5063/F1VD6WMF` (Céréghino 2018). Of these 852 taxa, 609 had measurements for dispersal and dormancy. We used this subset of taxa for the analysis.

The traits were measured categorically, as "none", "low", "intermediate", and "high" capacities for three traits: active dispersal, passive dispersal, and dormancy. We independently compared dormancy capacities with capacities for active and passive dispersal, and we computed the fraction of taxa that fit into all possible combinations of "none", "low", "intermediate", and "high" for both dispersal and dormancy.

C.2.2 Multivariate Analysis

We first standardized the trait measurements by converting the ordinal factors into ranks, assigning ties to average values (Podani 2005; Céréghino et al. 2018), using the decostand function of the R package *vegan* (Oksanen et al. 2019). We used *c*-means fuzzy clustering (with $k = 3$) to cluster the taxa into different dispersal-dormancy strategies (Kaufman and Rousseeuw 1990; Borcard et al. 2018), using the R package *cluster* (Maechler et al. 2018). We performed principal component analysis (PCA) on the rank-transformed trait data to reduce the dimensionality of the trait space, and we extracted the PCA loadings to explain the divergence among clusters. Taxa belonging to each cluster are listed in tables C.2, C.3, C.4, and C.5.

Table C.2: Taxa primarily belonging in Cluster 1.

Taxon	*n*
Chironomidae	38
Orthocladiinae	15
Tanypodinae	14
Platyhelminthes	12
Polypedilum	10
Hirudinea	9
Oligochaeta	8
Tanytarsus	5
Chironominae	4
Larsia	4
Metriocnemus	4
Chironomus	3
Elmidae	3
Elpidium	3
Monopelopia	3
Sphaeroceridae	3
Copepoda	2
Corynoneura	2
Dero	2
Dero superterrenus	2
Elpidium bromeliarum	2
Limnophyes	2
Naididae	2
Phytotelmatocladius delarosai	2
Pristina	2
Tanytarsus bromelicola	2
Aelosoma	1
Alona bromelicola	1
Annelida	1
Apocyclops	1
Aulophorus superterrenus	1
Boreochlus	1
Bryocamptus	1
Callistocypris mckenziei	1
Canacidae	1
Candonopsis kingsleyi	1
Ceriodaphnia	1
Ceriodaphnia laticaudata	1
Chironominae or Tanypodinae	1
Chironomini	1
Daphnidae	1
Elpidium maracaoensis	1
Eukiefferiella	1
Gravatamberus	1
Harnischia	1
Harpacticoida	1
Latinopsis	1
Paratanytarsus	1

Table C.2: Taxa primarily belonging in Cluster 1 (*Cont.*).

Taxon	*n*
Podonominae	1
Polypedilum kaingang	1
Polypedilum marcondesi	1
Pristina osborni	1
Rheocricotopus	1
Smittia	1
Stempellinella	1
Stenochironomus atlanticus	1
Tanytarsini	1

Table C.3: Subset of Cluster 1 taxa with high capacities for dormancy and passive dispersal.

Taxon	*n*
Copepoda	2
Alona bromelicola	1
Apocyclops	1
Bryocamptus	1
Ceriodaphnia	1
Ceriodaphnia laticaudata	1
Daphnidae	1
Harpacticoida	1

Table C.4: Taxa primarily belonging in Cluster 2.

Taxon	*n*
Diptera	42
Culex	28
Wyeomyia	24
Ceratopogonidae	22
Psychodidae	19
Toxorhynchites	17
Ephydridae	15
Bezzia	13
Telmatoscopus	8
Culicidae	7
Forcipomyia	7
Culicoides	3
Pericoma	3
Anophelinae	2
Culex albipes	2

Table C.4: Taxa primarily belonging in Cluster 2 (*Cont.*).

Taxon	*n*
Culex aphylactus	2
Culex imitator	2
Culicinae	2
Sphaeromias	2
Trichoptera	2
Alepia apexalba	1
Alepia zavortinkii	1
Anopheles bellator	1
Anopheles cruzzi	1
Anopheles homunculus	1
Anopheles kompii	1
Anopheles neivai	1
Anopheles or Wyeomia or Culex	1
Culex antillummagnorum	1
Culex bisulcatus	1
Culex carioca	1
Culex daumastocampa	1
Culex daumastocampa or jenningsi or rejector	1
Culex daumasturus	1
Culex davisi	1
Culex hedys	1
Culex inimitabilis	1
Culex jenningsi	1
Culex neglectus	1
Culex rejector	1
Culex shopei	1
Culex siphanulatus	1
Culex stonei	1
Culex worontzowi	1
Dasyhelea	1
Dasyheleniae	1
Haemagogus	1
Limatus durhami	1
Nematocera	1
Orthopodomyia	1
Phylloicus bromeliarum	1
Psychoda romeroii	1
Runchomyia frontosa	1
Stilobezzia	1
Toxorhynchites guadeloupensis	1
Toxorhynchites haemorroidalis	1
Toxorhynchites portoricensis	1
Toxorhynchites purpureus	1
Toxorhynchites solstitiales	1
Toxorhynchites theobaldi	1
Toxorhynchites trichopygus	1
Wyeomyia abebela	1
Wyeomyia abebela or ccircumcincta or melanopus	1
Wyeomyia aphobema	1

Table C.4: Taxa primarily belonging in Cluster 2 (*Cont.*).

Taxon	*n*
Wyeomyia circumcincta	1
Wyeomyia edwardsi	1
Wyeomyia edwardsi or mulhensi or theobaldi	1
Wyeomyia forattinii	1
Wyeomyia forcipenis	1
Wyeomyia greyii	1
Wyeomyia melanopus	1
Wyeomyia mitchellii	1
Wyeomyia mulhensi	1
Wyeomyia pallidoventer	1
Wyeomyia palmata	1
Wyeomyia pseudopecten	1
Wyeomyia splendida	1
Wyeomyia theobaldi	1

Table C.5: Taxa primarily belonging in Cluster 3.

Taxon	*n*
Cecidomyiidae	22
Forcipomyiinae	18
Syrphidae	18
Brachycera	17
Tipulidae	17
Coleoptera	16
Tabanidae	16
Scirtidae	15
Heteroptera	14
Atrichopogon	13
Corethrella	13
Empididae	11
Dolichopodidae	10
Copestylum	9
Trentepohlia	9
Dytiscidae	8
Hydrophilidae	7
Limoniinae	7
Sciaridae	6
Phoridae	5
Limoniidae	4
Stratiomyidae	4
Aedes	3
Corethrellidae	3
Meromacrus	3
Olbiogaster	3
Scirtes	3
Brachypremna	2

Table C.5: Taxa primarily belonging in Cluster 3 (*Cont.*).

Taxon	*n*
Ceratopogoninae	2
Coenagrionidae	2
Eristalinae	2
Eristalis	2
Hermetia	2
Lampyridae	2
Leptagrion andromache	2
Leptoconopinae	2
Microvelia	2
Polyphaga	2
Ptilodactylidae	2
Scatopsidae	2
Sphaeridiinae larva	2
Thaumaleidae	2
Aedes albopictus	1
aff. Drosophilidae	1
Anisopodidae	1
Aulacigaster	1
Axymyiidae	1
Bromeliagrion	1
Celina	1
Cheilotrichia	1
Contacyphon	1
Copelatus bimaculatus	1
Corethrella belkini	1
Corethrella fulva	1
Corethrella infuscata	1
Ctenophorinae	1
Fidena	1
Fidena rufopilosa	1
Gerridae	1
Hexatominae	1
Lejops barbiellinii	1
Leptagrion	1
Leptagrion bocainense	1
Leptagrion bocainense or macrurum	1
Leptagrion elongatum	1
Leptagrion macrurum	1
Leucotabanus	1
Limonia	1
Limoniini	1
Mecistogaster modesta	1
Mesoveliidae	1
Ocyptamus	1
Omicrus ingens adult	1
Omicrus ingens larva	1
Ormosia	1
Palpada	1
Paravelia	1

Table C.5: Taxa primarily belonging in Cluster 3 (*Cont.*).

Taxon	*n*
Periscelididae	1
Pipiza	1
Quichuana	1
Rhabdomastrix	1
Sphaeridiinae adult	1
Sphaerodinae	1
Stibasoma bicolor	1
Stibasoma fulvohirtum	1
Tipula	1
Tipulinae	1
Trentepohlia dominicana	1
Veliidae	1
Xilota	1
Zigoptera	1

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APPENDIX D

SUPPLEMENTAL INFORMATION FOR *METABOLIC INSIGHT INTO BACTERIAL COMMUNITY ASSEMBLY ACROSS ECOSYSTEM BOUNDARIES*

D.1 Sampling and environmental variables

Surface water samples were obtained approximately every 25 m along a longitudinal transect from the lacustrine zone near the dam to the two major streams feeding University Lake (Fig. D.1). We used a Quanta Hydrolab (OTT, Kempton, Germany) water sonde to measure temperature, dissolved oxygen, pH, and conductivity of the epilimnion at each site. We collected water samples at each site for biological and chemical analyses. We measured total phosphorus (TP) concentrations using the ammonium molybdate method (Wetzel and Likens 2000).

D.2 Sample preparation

For aquatic samples, we extracted total nucleic acids (RNA and DNA) from the filters using the MoBio PowerWater RNA extraction kit and the DNA elution accessory kit (Carlsbad, CA) and cleaned the extracts via ethanol precipitation. We treated RNA extracts with DNase (Invitrogen) to degrade DNA prior to cDNA synthesis via the SuperScript III First Strand Synthesis Kit and random hexamer primers (Invitrogen). For soil samples, we extracted DNA with the PowerSoil DNA isolation kit (MoBio, Carlsbad, CA). Once DNA and cDNA samples were cleaned and quantified, we amplified the 16S rRNA gene (DNA) and transcript (cDNA) using barcoded primers (515F and 806R) targeting the V4 hypervariable region (Caporaso et al. 2012). We purified sequence libraries using the AMPure XP purification kit (Bechman), quantified using the Quant-it PicoGreen dsDNA kit (Invitrogen), and pooled at equal molar ratios (final concentration:10 ng per library). After pooling, we sequenced the libraries on the Illumina MiSeq platform using 250 × 250 bp paired end reads (Reagent Kit v2) at the Indiana University Center for Genomics and Bioinformatics Sequencing Fa-

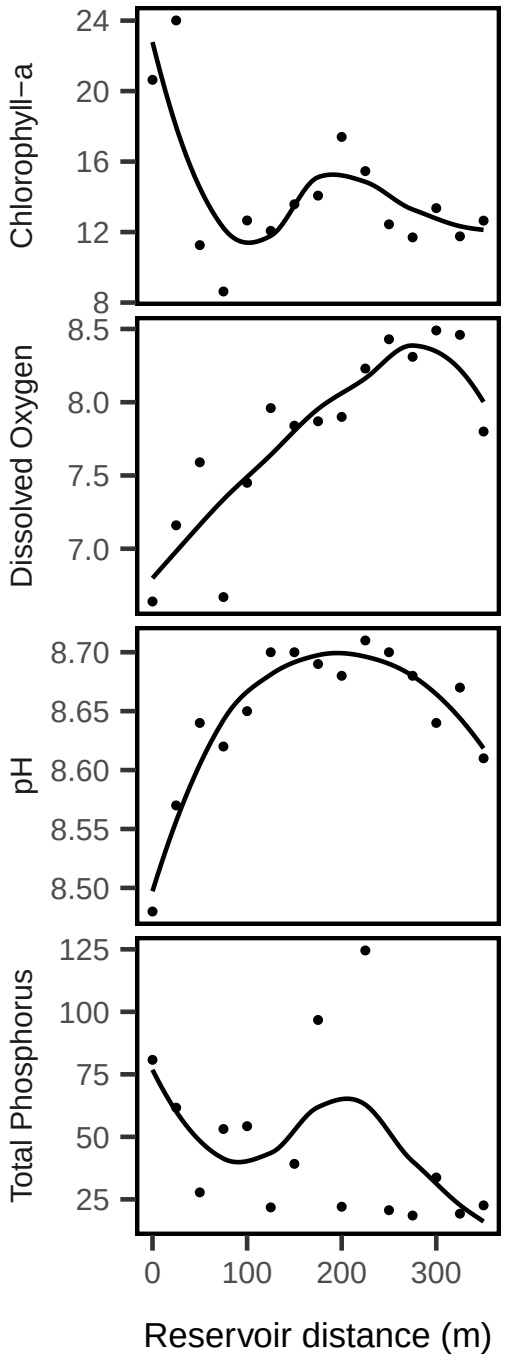

Figure D.1: Environmental variables across the University Lake transect fit with a loess smoother.

cility. Paired-end raw 16S rRNA sequences reads were assembled into contigs, quality-trimmed, and aligned to the Silva Database (version 132) (Quast et al. 2013). Chimeric sequences were detected and removed using the VSEARCH algorithm (Rognes et al. 2016). We created OTUs by first splitting the sequences based on the RDP taxonomy (Cole et al. 2009), and then binning sequences in to operational taxonomic units (OTUs) based on 97% sequence similarity. All initial sequence processing was completed using the software package mothur (version 1.41.1 Schloss et al. 2009).

D.3 Nestedness of aquatic OTUs

We partitioned β-diversity into turnover and nestedness components following Baselga (2010) using the 'betapart' R package (Baselga and Orme 2012). We used the Sørensen family of β-diversity metrics, and isolated the turnover and nestedness components of each aquatic sample (separated into DNA and RNA pools) relative to the three soil samples. We then averaged the turnover and nestedness fractions to produce a final mean nestedness and mean turnover value for each aquatic sample (Fig. D.2).

We also addressed nestedness more simply by creating a Venn diagram of OTUs from the soil community, the total aquatic community, and the active aquatic community to visualize the taxa shared between these portions of the meta-ecosystem (Fig. D.3).

D.4 Taxon trends in abundance along the transect

We summarize here information about the OTUs depicted in the main text. In particular, we list the taxa that decreased in relative abundance along the terrestrial-aquatic transect (Table D.1) and those that increased in relative abundance (Table D.2).

Table D.1: Taxa found in soils that get rarer along the transect (declining).

OTU	Slope	p-value	Phylum	Class	Order	Family	Genus
Otu00009	-5.12E-05	0.02755	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	*Pseudomonas*
Otu00010	-4.28E-05	0.5521	Proteobacteria	Unclassified	Unclassified	Unclassified	Unclassified
Otu00011	-1.93E-05	0.6012	Proteobacteria	Betaproteobacteria	Unclassified	Unclassified	Unclassified
Otu00018	-4.64E-05	0.02114	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	*Pseudomonas*
Otu00022	-2.50E-05	0.1182	Verrucomicrobia	Opitutae	Unclassified	Unclassified	Unclassified
Otu00028	-3.04E-05	0.02359	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	*Pseudomonas*
Otu00030	-2.22E-06	0.2763	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	*Micrococcus*
Otu00039	-8.51E-06	0.1787	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	*Comamonas*
Otu00045	-7.99E-06	0.5276	Proteobacteria	Betaproteobacteria	Burkholderiales	Oxalobacteraceae	Unclassified
Otu00059	-6.49E-05	0.02553	Actinobacteria	Actinobacteria	Actinomycetales	Micrococcaceae	*Arthrobacter*
Otu00065	-5.54E-05	0.02116	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Sphingobacteriaceae	*Pedobacter*
Otu00072	-1.88E-05	0.09149	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	*Sphingomonas*
Otu00077	-5.84E-05	0.01187	Bacteroidetes	Flavobacteriia	Flavobacteriales	Flavobacteriaceae	*Flavobacterium*
Otu00086	-1.26E-05	0.03621	Proteobacteria	Alphaproteobacteria	Rhizobiales	Bradyrhizobiaceae	*Bradyrhizobium*
Otu00094	-2.21E-05	0.03169	Proteobacteria	Betaproteobacteria	Burkholderiales	Oxalobacteraceae	*Duganella*
Otu00095	-3.56E-05	0.03614	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Unclassified
Otu00170	-2.48E-05	0.02878	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Sphingobacteriaceae	Unclassified
Otu00545	-1.25E-06	0.02985	Actinobacteria	Actinobacteria	Solirubrobacterales	Solirubrobacteraceae	*Solirubrobacter*

Table D.2: Taxa found in soils that get more common along the transect (maintained).

OTU	Slope	p-value	Phylum	Class	Order	Family	Genus
Otu00001	1.44E-05	0.07999	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Unclassified
Otu00002	0.0002104	0.002237	Actinobacteria	Actinobacteria	Actinomycetales	Unclassified	Unclassified
Otu00003	9.85E-05	0.006441	Verrucomicrobia	Spartobacteria	Unclassified	Unclassified	Unclassified
Otu00005	3.59E-05	0.01737	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Chitinophagaceae	*Sediminibacterium*
Otu00006	6.52E-06	0.1618	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Saprospiraceae	Unclassified
Otu00012	7.57E-06	0.09905	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	Unclassified
Otu00014	8.42E-05	0.0007891	Actinobacteria	Actinobacteria	Actinomycetales	Unclassified	Unclassified
Otu00023	3.48E-07	0.8	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Moraxellaceae	*Acinetobacter*
Otu00029	3.30E-05	0.004456	Actinobacteria	Actinobacteria	Actinomycetales	Unclassified	Unclassified
Otu00032	3.59E-06	0.8341	Bacteroidetes	Unclassified	Unclassified	Unclassified	Unclassified
Otu00033	9.09E-06	0.7085	Proteobacteria	Alphaproteobacteria	Rhizobiales	Unclassified	Unclassified

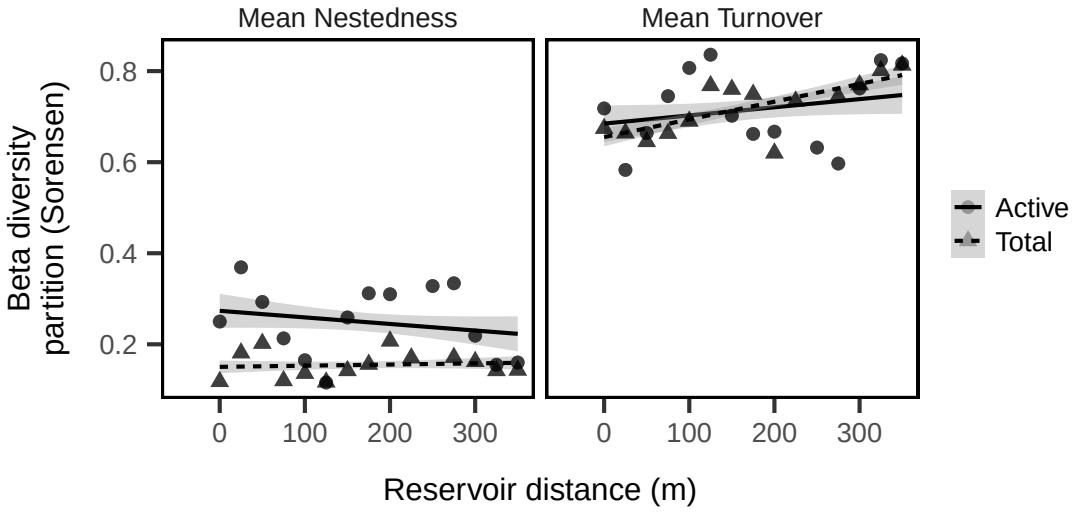

Figure D.2: Partitioning β-diversity into nestedness and turnover components in the aquatic samples relative to the terrestrial soil samples. Partitioning was done on the Sørensen dissimilarity index, a presence-absence analogue of the Bray-Curtis dissimilarity used in the main figures. Note that the main text converted the dissimilarity values to similarity, but here, the partitions of Sørensen index remain partitions of a dissimilarity metric and therefore represent community differences due to nestedness and turnover components.

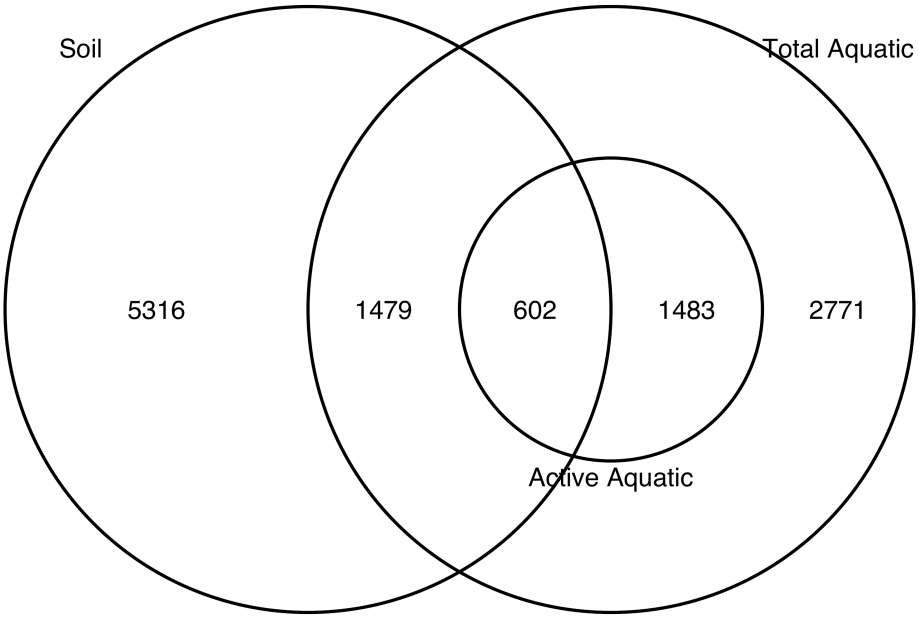

Figure D.3: Overlap of OTUs between the different subsets of the meta-ecosystem. Of the 7397 OTUs detected in the soil samples, 28% (n = 2081) were detected in the aquatic samples, and only 8% (n = 602) were detected in an active state. Of the 6335 OTUs detected in the total aquatic community, 32% (n = 2081) were also detected in soils, and 67% were not detected in soils. Of the 2085 OTUs in the active aquatic community, 29% were detected in soils, while 71% were not.

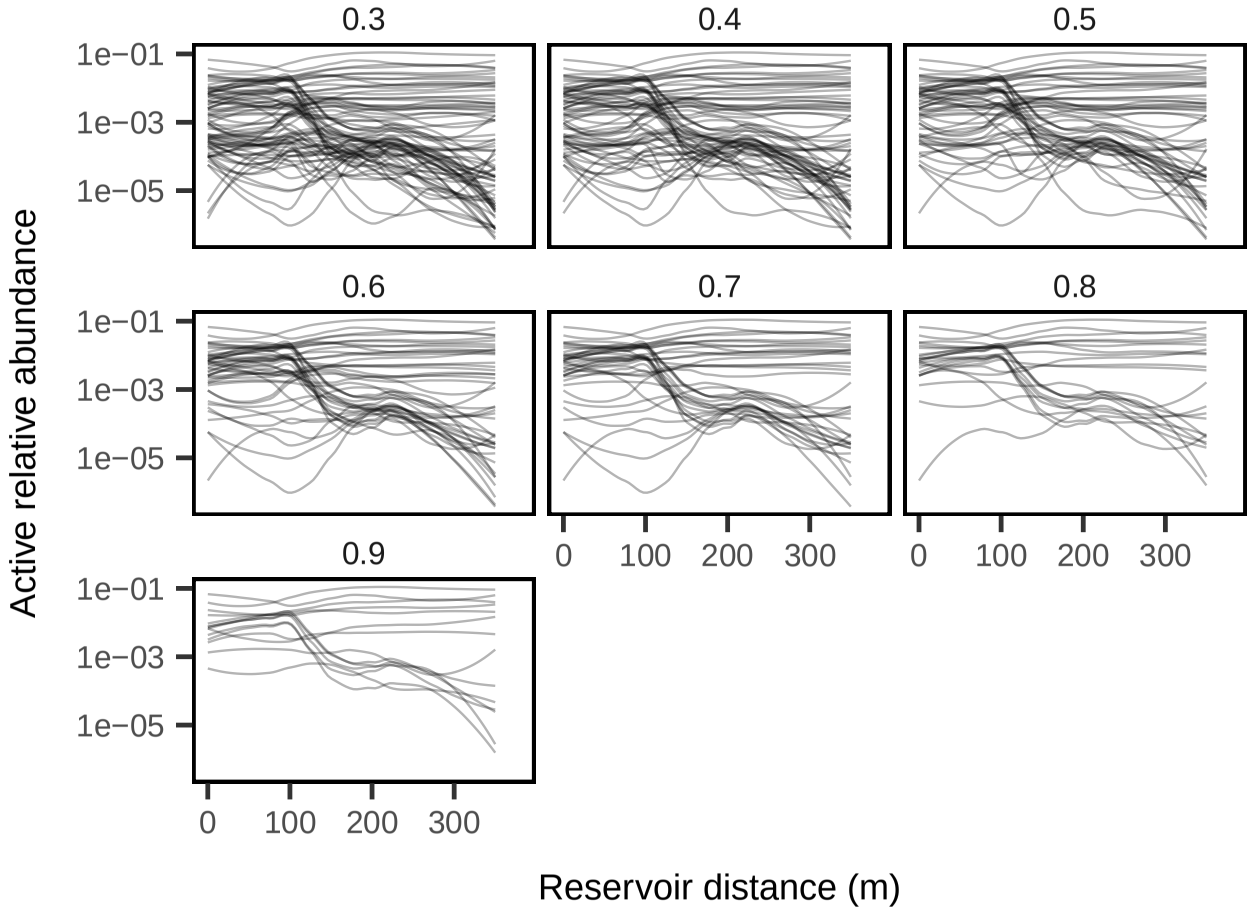

Figure D.4: Sensitivity of terrestrial-derived OTU fate to threshold of OTU incidence cutoff (minimum fraction of sites detected). We present cutoff of 0.75 in the main text, but qualitative conclusions remain consistent across thresholds, with some taxa declining and others maintained along the gradient.

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Sokol, E.R., **N.I. Wisnoski**, C.M. Swan, R. Andrade, H.L. Bateman, A.G. Hope, J. Kominoski, N.K. Lany, L. Marazzi, S.J. Presley, A. Rassweiler, S. Record, M.R. Willig, and P.L. Zarnetske. 2017. *The role of long-term ecological research programs for testing metacommunity theory and understanding biodiversity patterns.* Ecological Society of America Annual Meeting. Portland, OR.

Voelker, N.M., E.R. Sokol, **N.I. Wisnoski**, C.M. Swan, T. Lamy, M.C.N. Castorani, L. Marazzi, A. Compagnoni, J.R. Blanchard, R. Andrade, and N.K. Lany. 2017. *Evaluating the link between metacommunity stability and environmental variability across trophic groups represented at LTER sites.* Ecological Society of America Annual Meeting. Portland, OR.

Wisnoski, N.I. and J.T. Lennon. 2016. *Community assembly processes differ between surface water and sediment-associated communities in stream networks.* Ecological Society of America Annual Meeting. Fort Lauderdale, FL.

Wisnoski, N.I. and J.T. Lennon. 2016. *Local and regional processes in stream microbial community assembly (poster).* International Symposium on Microbial Ecology (ISME 16). Montreal, QC.

Wisnoski, N.I., A.S. Ward, and J.T. Lennon. 2015. *Bacterial metacommunity structure across a stream network (poster).* LTER All Scientists Meeting. Estes Park, CO.

TEACHING

Co-Instructor. BIOL-Z 620: Quantitative Biodiversity. *Indiana University.* Spring 2017.

Associate Instructor. BIOL-L 111: Foundations of Biology: Diversity, Evolution, and Ecology. *Indiana University.* Spring 2016, Fall 2016, Spring 2018, Spring 2019, Spring 2020.

Associate Instructor. BIOL-L 113: Biology Laboratory. *Indiana University.* Fall 2014, Fall 2017, Fall 2018, Fall 2019.

Grader. BIO 364: Microbial Ecology. *University of Texas.* Spring 2014.

Teaching Assistant. SSC 328M: Biostatistics. *University of Texas.* Spring 2013, Fall 2013.

WORKSHOPS

Lead Organizer. 2018. Synthesizing long-term community data: questions, challenges, and advances. LTER All Scientists Meeting. Pacific Grove, CA.

PEER REVIEWER

Peer reviewer for the following journals: Aquatic Ecology, BioScience, Ecology, Ecology Letters, Environmental Microbiology, and Journal of Biogeography.

MENTORSHIP AND SERVICE

Undergraduate and Summer REU STEM Mentor	Jan 2015 – 2020
High School STEM Mentor *Jim Holland Summer Scholars Program*	Summer 2015 – 2020
Coordinator, High School Riverwatch Sampling *Jim Holland Summer Enrichment Program*	Summer 2017 – 2019
EcoLunch Co-Organizer	August 2015 – May 2016
Metacommunity Reading Group Organizer	Summer 2015

COMPUTATIONAL SKILLS

R, python, bash, Mathematica, LaTeX, markdown, git/GitHub

PROFESSIONAL SOCIETY MEMBERSHIP

Ecological Society of America
Society for Freshwater Sciences
American Society of Naturalists